

ADAPT, MOVE OR PERISH
THE INTERACTION OF GENETICS AND DEMOGRAPHY
IN FRAGMENTED POPULATIONS UNDER CLIMATE CHANGE

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ABSTRACT

Habitat loss and degradation, and human-induced climate change are two of the main current threats to biodiversity. While the impacts of these pressures separately on species survival are being investigated extensively, we have only just begun to unravel the combined impact of these two pressures on species. The combination of range shifts and local adaptation has been suggested to increase species survival under climate change. Habitat fragmentation may increase the rate of local adaptation due to reduced genetic variation as a result of declined population sizes, but also enhances the impact of stochastic processes such as founder effects. A quantification of each of these processes and their combined outcome is therefore necessary to assess the chances of species survival and fitness under different conditions. In this thesis I have used a spatially explicit, individual-based eco-evolutionary model to investigate the interaction of founder events and local adaptation throughout a range of the middle spotted woodpecker (*Dendrocopus medius*) in fragmented habitat under climate change. This is a species with an average performance regarding dispersal distance and population growth rate. In Chapter 2 I show that consecutive founder effects occur at all projected levels of temperature increase, in time causing range-wide loss of neutral genetic diversity. In Chapter 3 I demonstrate that increased habitat area prolongs the conservation of neutral genetic variation under range shift but does not prevent the depletion of the genetic variation in the populations that are newly established. Founder events thus have important consequences for the level and distribution of neutral genetic variation in species of average dispersal capacity. In Chapter 4 I show that the founder effect is also a major component of the evolutionary process during a range shift of a species that features genetic differences between central and marginal populations in fragmented habitat. This eventually leads to maladaptation in the range centre and to a decrease of the species' survival probability. In Chapter 5 I demonstrate that founder effects greatly enhance local adaptation towards increased dispersal in new populations at the expanding range margin. When the selection pressure in these populations changes at a later stage, the local depletion of functional genetic variation caused by the founder event results in delayed adaptation and thus decreased survival probability of the metapopulation. This finding indicates that it is of great importance to assess the relative contribution of founder effects in evolutionary processes in populations established beyond the original range limit under range shift, especially in fragmented habitat. While founder effects have been clearly associated with the patterns in neutral genetic diversity observed after range expansions, studies showing trait evolution under range shifts have thus far not investigated the potential role of founder effects. I advocate the further development of realistic, species-specific eco-evolutionary models to increase both understanding and predictive power of the interaction of demographic and genetic responses of species to combined pressures of habitat fragmentation and climate change. I further recommend that empirical studies combine the investigation of changes in adaptive traits with the assessment of signatures of founder effects, which can be uncovered using neutral markers, both in the same individuals. If local adaptation shows to be enhanced by founder effects, the long-term adverse effects of reduced genetic diversity should be quantified and taken into consideration.

CHAPTER ONE

INTRODUCTION

Species in the Anthropocene

Our planet is inhabited by 7 billion people. For our housing, feeding, transport and other needs we use a vast amount of space and natural resources. The conversion of natural areas into cities, agricultural land, roads and industrial sites, and the exploitation of natural resources have led to large changes in the surface of the Earth as well as in its atmosphere, waters and soil. These changes have an impact on the survival of many species in natural environments, while the capacity of the Earth to sustain us in the future depends of these species (Isbell *et al.* 2011, MEA 2005). Habitat loss and degradation, and human-induced climate change are two of the main current threats to biodiversity (IUCN 2011). While the impacts of these pressures on species survival are being investigated extensively, we have only just begun to unravel the complex interactions between the various responses of species to the combination of both pressures (see Figure 1.1).

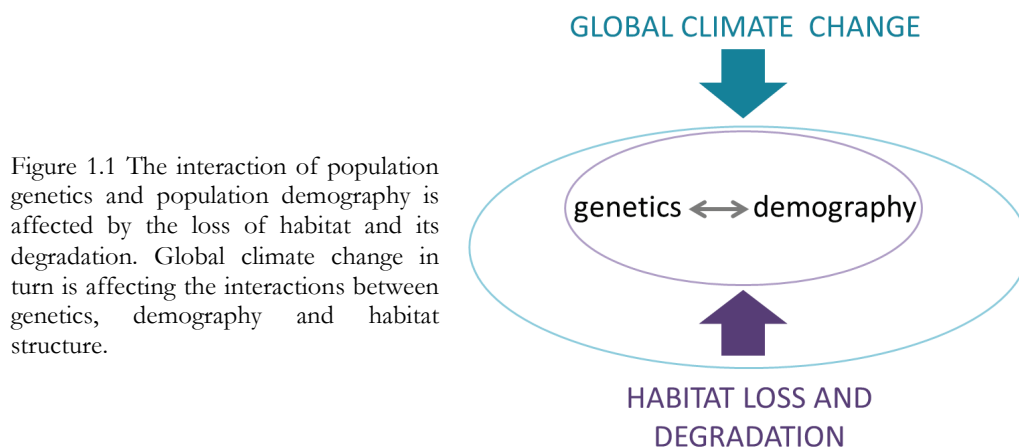


Figure 1.1 The interaction of population genetics and population demography is affected by the loss of habitat and its degradation. Global climate change in turn is affecting the interactions between genetics, demography and habitat structure.

The effects of habitat fragmentation on population demography and genetics

Habitat loss and fragmentation lead to smaller population sizes and increased isolation of natural populations of species. Small populations are more prone to extinction as a result of environmental stochasticity, while increased isolation hampers the arrival of immigrants from other populations. Both the population rescue and the recolonisation of the habitat patch are thus increasingly impeded by habitat fragmentation, leading to an average overall declined persistence of populations and species (Andren 1994).

The decrease of population size also has genetic consequences. Small populations can only sustain a low level of genetic diversity, which has implications for their evolutionary potential (Booy *et al.* 2000, Frankel 1974, Willi *et al.* 2006). A small population is more prone to genetic drift, and this can eventually lead to the accumulation of mildly deleterious mutations (Lande 1995, Lynch *et al.* 1995), causing decreased fitness and survival. Inbreeding depression is the loss of fitness due to increased homozygosity as a result of breeding among relatives, which is more likely under decreasing population sizes (Crnokrak & Roff 1999). The adverse genetic consequences of a reduced population size may be relieved by the immigration of individuals from other populations (Tallmon *et al.* 2004, Vila *et al.* 2003). Increased isolation of populations as a result of habitat fragmentation however hampers this process, and leads to increased genetic differentiation among populations. Genetic differentiation of populations

may also arise upon the colonisation of an empty habitat patch by a few founding individuals (Mayr 1942). After such a founder event the genetic variation of the newly established population differs from the ancestral population or populations due to the sampling error resulting from the small number of founders (Lee 2002).

Any observed genetic differentiation between populations is thus the result of local adaptation, genetic drift, and/or founder events. In the case of local adaptation, increased gene flow among populations may have an adverse effect because it impedes the adaptation process through gene swamping (Bridle & Vines 2007), or eliminates the adaptation in the event of outbreeding depression (Tallmon *et al.* 2004). In such cases, increasing the connectivity between isolated populations has undesired consequences. In the case that the observed genetic differentiation between populations is a result of drift or founder events, increased gene flow may be beneficial for the survival of these populations. However, as reduced genetic variation may enhance local adaptation as well (Tsutsui *et al.* 2000), the optimal population sizes and levels of gene flow among populations depend on the interaction of specific life history traits and both past and present spatial characteristics. Assessments of viable population sizes and necessary numbers of dispersers therefore require species- and location-specific ecological and landscape information.

Demographic and genetic responses to climate change

In response to contemporary climate change many species across the globe are currently showing geographical range expansions or range shifts (Chen *et al.* 2011, Parmesan & Yohe 2003, Root *et al.* 2003). A range *shift* requires two phenomena. It consists of an expansion of the species' range at the range limit where changing climate conditions allow population establishment beyond the original range edge. Besides, it requires a retraction of the species' range by the extinction of populations at the range margin where the conditions gradually drop below the survival threshold. In areas where a species' range has been expanding, its populations may show a clear genetic signature of low genetic diversity due to consecutive founder events (Balint *et al.* 2011, Excoffier *et al.* 2009, Garroway *et al.* 2011, Hill *et al.* 2011). Hewitt (1996) investigated the current genetic patterns of species that had expanded their ranges after the last glacial maximum, and showed that such genetic signatures may be very persistent. A pattern of lower genetic diversity is however not always present upon range expansion. Lineages migrating along different routes can arrive in the same area and merge (Hewitt 1996). In invasive species the founder effect can be diluted through multiple introductions (Roman 2006) or as a result of the specific dispersal strategy (Bronnenhuber *et al.* 2011).

In addition to the demographic response of species to contemporary climate change, and its consequences for the levels of genetic diversity in newly established populations, species have shown adaptive responses to the changing climate conditions. They are either directly adapting to warmer conditions (Jump *et al.* 2006, Parmesan 2006), or indirectly, through the evolution of resource use and dispersal at expanding range margins (Hill *et al.* 2011, Parmesan 2006, Thomas *et al.* 2001). Observed rapid adaptations have been the result of changes in local gene frequencies (Jump *et al.* 2006). Thus far there has been no indication that new mutations have led to species-wide increased climate tolerances (Parmesan 2006).

Under range shift, populations at the expanding range margin may eventually become located at the species' range centre or even at the retracting range margin. The decline of genetic diversity under range expansion implies that the populations in the original species' range are the storage rooms for most of the existing genetic diversity in such a species (Hampe & Petit 2005, Hewitt 1996, McInerny *et al.* 2009). However, the demographic and genetic processes at the retracting range margin have so far been relatively little investigated (Hill *et al.* 2011). Arenas *et al.* (2011) observed in a modelling study that fast range retractions rather counter-intuitively preserve higher levels of genetic diversity than slow retractions. The importance of the populations in the original species' range, combined with these surprising findings about processes at the retracting margins, together indicate that the main current research focus on expanding range margins is likely to gain insufficient understanding to conserve the genetic diversity of species under climate change (Hill *et al.* 2011).

Responding to global climate change in fragmented habitat

Many species currently fail to synchronise their ranges with their required climate conditions (Chen *et al.* 2011). The risk of failure is expected to increase if the shift of the species' range is hampered by the fragmentation of its habitat (Opdam & Wascher 2004, Schippers *et al.* 2011, Travis 2003). It has been suggested that the combination of range shifts and local adaptation towards higher frequencies of beneficial genes may increase species survival under climate change (Hoffmann & Sgro 2011, Parmesan 2006). As observed above, habitat fragmentation may increase the rate of local adaptation due to reduced genetic variation as a result of declined population sizes (Tsutsui *et al.* 2000), but also enhances the importance of stochastic processes such as genetic drift and founder effects. A quantification of each of these processes and their combined outcome is therefore necessary to assess the chances of species survival and fitness under different conditions. Empirical studies into evolutionary processes under climate change in fragmented habitat encounter the outcome of the interaction of all these processes, but have thus far not been capable of assessing their relative importance on the results (Hill *et al.* 2011, Jump *et al.* 2006, Parmesan 2006, Thomas *et al.* 2001). For example, Thomas *et al.* (2001) show the increase of the variety of suitable habitat types for two butterfly species, and the increased fractions of longer-winged individuals of two bush cricket species in recently founded populations. However, which processes had caused this evolutionary response remained unclear. Theoretical and simulation studies can systematically investigate the interactions of different model processes, but the application of their results is restrained by the availability and use of ecological and spatial parameters (Arenas *et al.* 2011, McInerny *et al.* 2009, Travis *et al.* 2007). Travis *et al.* (2007) for instance show that founder events can in theory cause a deleterious mutation to reach high densities in newly founded populations. Under which conditions we may expect such a phenomenon in the field can however not be answered. A study by Hanski and Mononen (2011) about an eco-evolutionary model of dispersal in spatially heterogeneous environment that has been tested on empirical data, demonstrates the strength of the combination of both techniques. The study increases the understanding of the effects of habitat loss and fragmentation on the evolution of dispersal. However, it does not include influences of climate change and ignores founder effects. The interaction of demographic and genetic species' responses to climate change in fragmented habitat and their effect on eventual species survival and fitness have thus

medius), living in fragmented habitat and affected by climate change. This is a species with an average performance regarding dispersal distance and population growth rate. It was therefore suitable for the investigation of the research question and additionally allowed a generalisation of the results to a wider range of species. I incorporated life history parameters based on empirical data to increase the realism and therefore applicability of the model results. The climate change parameters incorporated both global warming from realistic scenarios and increased weather variability at different levels. This allowed interactions between these climate change effects to be evaluated as well.

RESEARCH QUESTIONS AND THESIS OUTLINE

Many studies, both theoretical (McInerny *et al.* 2009) and empirical (Balint *et al.* 2011, Garroway *et al.* 2011, Hewitt 1996) have shown reduced levels of genetic variation in newly established populations under species' range expansion in response to climate change. This is the result of consecutive founder events. However, none of the theoretical studies have attempted to make a species-specific assessment of the range-wide consequences of such founder effects under projected levels of contemporary climate change in a spatially irregular landscape. In *Chapter 2* I therefore ask: *How does the shift of range affect the level and distribution of the neutral genetic diversity across a species range in a fragmented habitat under projected levels of temperature increase?* This chapter shows that consecutive founder effects occur at all projected levels of temperature increase, in time causing range-wide loss of neutral genetic diversity.

Monitoring of the level of genetic variation and management strategies for its *in situ* conservation have hardly been investigated for natural populations (Laikre *et al.* 2010). Strengthening the habitat network by increasing patch sizes and connectivity between patches has been proven to increase metapopulation size and survival probability (Fischer & Lindenmayer 2007, Opdam *et al.* 2003). Thus in *Chapter 3* I ask: *Does landscape structure affect the survival of neutral genetic diversity under a climate change-induced range shift?* In this chapter I observe that increased habitat area prolongs the conservation of species-wide neutral genetic variation under range shift but does not prevent the depletion of the genetic variation in the newly established populations. Founder events thus have important consequences for the level and distribution of neutral genetic variation in species of average dispersal capacity across the investigated range of habitat patch numbers and sizes in fragmented landscapes.

Many species ranges are located along a biogeographical gradient and show genetic differences between central and marginal populations (Sexton *et al.* 2009). Evolution under climate change has been shown to occur through the frequency increase of beneficial genotypes (Jump *et al.* 2006), but the relative importance of local adaptation and founder events under range shift have thus far not been investigated. Therefore I ask in *Chapter 4*: *What are the consequences of the interaction of local adaptation and founder effects during a range shift of a species that features genetic differences between central and marginal populations in fragmented habitat?* It shows that in this interaction the founder effect is dominating the process of local adaptation, and that eventually leads to maladaptation in the range centre and to a decrease of the species' survival probability.

Some studies have shown evolutionary changes in the dispersal rates of populations at the expanding species' range margin, allowing increased expansion rate under climate change (Parmesan

2006). These studies have not considered the possibility that founder events can play an important role in shaping the genetic composition of newly established populations. In *Chapter 5* I therefore ask: *Can increased dispersal at the expanding range margin in fragmented habitat be the result of founder effects?* This chapter shows that founder effects greatly enhanced local adaptation in new populations at the expanding range margin. When the selection pressure in these populations changes at a later stage, the local lack of genetic variation caused by the founder event results in delayed adaptation and thus decreased survival probability of the species.

In *Chapter 6* I give a short overview of the results of these studies and synthesise their scientific implications in view of the relevant literature. Besides, this chapter gives a discussion of the methodological constraints and provides perspectives and ideas for further research. Lastly, I suggest some implications of my results for nature policy.

CHAPTER TWO

PROJECTED CLIMATE CHANGE CAUSES LOSS AND REDISTRIBUTION OF NEUTRAL GENETIC DIVERSITY IN A MODEL METAPOPULATION OF A MEDIUM-GOOD DISPERSER

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ABSTRACT

Climate change causes species ranges to shift geographically as individuals colonize new suitable temperature zones or fail to reproduce where climate conditions fall below tolerance levels. Little is known about the potential loss of genetic diversity in such dynamic ranges. We investigated the level and distribution of neutral genetic diversity in shifting metapopulations during three scenarios of temperature increase projected for this century and at various degrees of weather variability. We used an individual-based and spatially explicit metapopulation model in which temperature zones were simulated to move across a fragmented landscape following different climate change scenarios. Although the connectivity between habitat patches allowed the species, modelled after the middle spotted woodpecker *Dendrocopos medius*, to move along with the shifting temperature range, existing neutral genetic diversity was lost under all three temperature increase scenarios. This was independent of the loss of individuals. The explanation for this effect is that only a part of the original genetic variation moved into the newly colonised habitat. Under increased weather variability the number of individuals and the number of alleles per locus were persistently lower. However, the pattern of changes in allele distributions under temperature zone shifts was the same under all weather variability levels. Genetic differentiation between populations had a tendency to increase at metapopulation range margins, but decreased again when population sizes increased in time. Increased weather variability led to increased variation around the mean genetic differentiation across the metapopulation. Our results illustrate the usefulness of more realistic models for studying the effects of climate change on metapopulations. They indicate that biodiversity monitoring indices based on species occurrence and abundance are not a good proxy for the trend in the level of genetic diversity. Further, the results underline the importance of conserving areas where species have existed for a long time as modern refugia for genetic diversity.

INTRODUCTION

Adoption of the Convention on Biological Diversity at the 1992 Earth Summit in Rio de Janeiro has led to a worldwide commitment to sustain the diversity of life on Earth. This has resulted in widely used biodiversity monitoring tools and conservation programmes. One of the threats to biodiversity are current climatic changes (IUCN in Foden *et al.* 2008), reflected in increased temperature and increased weather variability (IPCC 2007). Increased temperature may cause a shift of species ranges when species follow suitable temperature zones (Parmesan 2006, Parmesan & Yohe 2003, Root *et al.* 2003). Relatively rapid climate change may cause extinctions of species that are not able to track suitable conditions due to limited dispersal capacities (Schippers *et al.* 2011). On top of this, movement of individuals and hence also range shifts can be hampered by fragmentation of habitat (Opdam & Wascher 2004, Travis 2003, Vos *et al.* 2008, Warren *et al.* 2001).

Additionally, range shifts have population genetic consequences. If expansion at the leading edge of the range occurs through a sequence of founder effects, this results in a reduction of genetic diversity in the newly colonized habitat (Austerlitz *et al.* 1997, Hewitt 1996, Hewitt & Nichols 2005, Nei *et al.* 1975, Neve *et al.* 2009). Therefore, after a period of range expansion, genetic diversity in a species range is decreasing from the rear edge to the leading edge (Hewitt 1996, McNerny *et al.* 2009). This has been shown in a strategic model of the fate of mutations during population expansion into new habitat (McInerny *et al.* 2009). It has also been shown to be the general pattern in several groups of species as a consequence of range expansion across central and northwestern Europe after the last ice age (Hewitt 1996).

Range *shifts* are different from range expansions since there is also a range retraction at the trailing edge to consider. McNerny *et al.* (2009) showed in a modelling approach that survival of neutral mutations at the trailing edge is reduced as a result of decreasing habitat suitability.

The predicted increased weather variability may increase population extinction rates (Lande 1993, Leigh 1981, Saether *et al.* 1998, Verboom *et al.* 2010) and thus lead to an increase in number of founder events under range shifts through enhanced extinction-colonisation cycles. This would have consequences for the level of genetic diversity in newly colonised regions. Besides, this effect may be enhanced by decreased habitat size and increased habitat isolation resulting from habitat fragmentation.

From the above we conclude that the currently predicted climate change may affect the genetic diversity of species (Hewitt & Nichols 2005, McNerny *et al.* 2009). However, projections of future climate, including both temperature and weather variability increase, have not yet been incorporated in studies modelling the effects on species' genetic diversity. Existing models have thus so far also taken a more strategic approach, using non-specific, simplified assumptions about species' demography and genetics. Besides, spatial irregularity in habitat configurations has not been incorporated into these strategic studies. See e.g. McNerny *et al.* (2009), who included range shifts but limited their study to clonal haploid reproduction and a landscape grid with population sizes 0 or 1. Edmonds *et al.* (2004) studied range expansion only. They allowed population growth but limited themselves to clonal haploid reproduction and a landscape grid. Klopstein *et al.* (2006) used a landscape grid and haploid individuals under range expansion as did Travis *et al.* (2007). Bruggeman *et al.* (2010) did study the effects of habitat

loss and fragmentation on genetic variation in a complex model based on realistic ecological and population genetic data in irregular landscapes. Yet this study was not focused on changing species' ranges.

In this paper we explore how range shifts induced by the predicted climate change will affect the level and distribution of neutral genetic diversity in a species range. We chose a more complex approach in an attempt to realistically model a specific species, the middle spotted woodpecker (*Dendrocopos medius*). This species has a medium dispersal capacity, with an average yearly dispersal distance in the same order of magnitude as the yearly temperature zone shift. We used an individual-based and spatially explicit metapopulation model in which temperature zones were simulated to move across a fragmented landscape following different scenarios for predicted climate change (HadleyCentre 2003). Since we are interested in the demographic effects of climate change on genetic diversity, we investigated neutral genetic diversity only to not confuse genetic signatures of range shifts with signatures of selection (Excoffier *et al.* 2009, Excoffier & Ray 2008). We expected that in the newly colonised areas, allelic diversity will decrease and genetic differentiation between populations will increase (Eckert *et al.* 2008). Further, we expected that both trends may be correlated with temperature increase and increased weather variability. To investigate these expectations we specifically asked how:

- 1) predicted temperature increase, and

- 2) predicted temperature increase combined with increased weather variability

affect the level and distribution of neutral genetic diversity in the species range in time. Building on both the above mentioned studies into population genetics and on frequently used climate-envelope models (e.g. Settele *et al.* 2008), we believe our modelling approach is a further step towards more realistic species-specific assessments of climate change effects (Scoble & Lowe 2010).

METHODS

For this study we used METAPHOR, a simulation model for metapopulation demography (Verboom *et al.* 2001, Vos *et al.* 2001b). The model has been extended to allow for temperature zone shifts and weather variability by Schippers *et al.* (2011). Here a new extension provided each individual in this study with a genome of 10 unlinked diploid genes (representing 1 locus at each of 10 different chromosomes). Population genetics in our model was the result of population demography. There was no reciprocal effect of genetics on demography, thus all genes were neutral. Reproduction, dispersal and survival were based on population density and habitat quality. Habitat quality was controlled by time and location specific temperature. As such we simulated the effect of stochastic temperature zone shifts on neutral genetic diversity. For detailed information see Appendix 2.1: Detailed model description and Appendix 2.2: Genetic make-up and protocol. Table 2.1 gives an overview of all species, gene and climate parameters used.

The landscape we used in the model had dimensions of 15 km from east to west by 2000 km from north to south. The east and west side were merged to create a cylindric landscape. The landscape contained 3000 circular habitat patches of 50 ha each, so consisted of a total of 5% habitat. Patches were placed in random positions in the landscape, yet only allowed if they were at a minimum distance

of 150 m from existing patches. Five landscape variants with different habitat positions were randomly generated and each simulated parameter setting was repeated twice in each landscape variant.

Table 2.1. Model parameters used. Species and climate parameters are those used by Schippers *et al.* (2011). Parameter names link this table to the functions in Appendix 2.1: Detailed model description.

Parameter description	Value	Unit	Parameter name
Landscape parameters			
number of patches	3000		
patch area	50	ha	
patch carrying capacity	20	individuals	
Species parameters			
<i>Recruitment</i>			
area per reproductive unit	5	ha	
recruitment at density = 0 and quality = 1	2.4	juveniles/female	N_{O_PD0HQ1}
recruitment at density = 1 and quality = 1	1.8	juveniles/female	N_{O_PD1HQ1}
recruitment at density = 0 and quality = 0	0	juveniles/female	N_{O_PD0HQ0}
<i>Dispersal</i>			
maximum dispersal distance	15	km	
maximum detection distance	150	m	l
juvenile dispersal probability			
at density = 0 and quality = 1	0	year ⁻¹	P_{D_PD0HQ1}
at density = 1 and quality = 1	0.6	year ⁻¹	P_{D_PD1HQ1}
at density = 0 and quality = 0	1	year ⁻¹	P_{D_PD0HQ0}
adult dispersal probability			
at density = 0 and quality = 1	0	year ⁻¹	P_{D_PD0HQ1}
at density = 1 and quality = 1	0.1	year ⁻¹	P_{D_PD1HQ1}
at density = 0 and quality = 0	0.5	year ⁻¹	P_{D_PD0HQ0}
<i>Survival</i>			
juvenile survival probability	1	year ⁻¹	P_{S_PD0HQ1} , P_{S_PD1HQ1} , P_{S_PD0HQ0}
adult survival probability at quality = 1	0.8	year ⁻¹	P_{S_PD0HQ1} , P_{S_PD1HQ1} , P_{S_PD0HQ0}
adult survival probability at quality = 0	0.55	year ⁻¹	P_{S_PD0HQ0}
Genetic parameters			
allele range at initialisation	1-20		
allele range after mutation	21-50		
mutation rate	10 ⁻⁴	generation ⁻¹	
Climate parameters			
temperature isocline speed	2, 4, 8	km year ⁻¹	T
weather variability	0, 140, 280	km	σ_d
temperature tolerance	800	km	H
initial temperature optimum location	400	km from the south edge	$Y_{opt,0}$
Model run parameters			
burn-in	3000	years	
investigated time points after burn-in	0, 25, 50, 75, 100, 125, 150, 200, 250, 300, 400, 500, 600	years	

We modelled a woodland bird, parameterised as the middle spotted woodpecker (*Dendrocopus medius*). Parameters were based on biological information (Hagemeijer & Blair 1997, Kosenko & Kaigorodova 2001, Kosinski *et al.* 2004, Kosinski & Ksit 2006, Michalek & Winkler 2001, Pasinelli 2000, Pettersson 1985a, Pettersson 1985b) and on the interpretation by Schippers *et al.* (2011) (see Table 2.1). The model distinguished two sexes and two lifestages. Recruitment, dispersal and survival were all dependent of population density and habitat quality. From their origin patch individuals could disperse in every direction, along a straight line. Connectivity to other patches was determined by destination patch radius and by distance from original to destination patch. The maximum dispersal distance was 15 km, so habitat patches that were separated by more than this distance were not connected at all. Our model did not allow dispersers to ignore a nearer patch, so more distant patches are located in the shadow of the nearer patch. An individual may arrive in a patch with a population size larger than carrying capacity twice per dispersal event, and was then allowed to disperse again. Should it fail to reach a habitable patch within three dispersal rounds, it would die.

The climate optimum was shifting northwards according to the temperature increase scenario used (see below and Table 2.1). The weather variability was simulated by the standard deviation of the average temperature (see below and Table 2.1). Climate suitability was translated to a habitat patch quality ranging from 0 to 1, based on distance from the climate optimum and on the half value parameter used, following a Gaussian curve (see Schippers *et al.* 2011). We used three temperature isocline speed scenarios, based on work by the Hadley Centre (2003). The first scenario was a temperature increase of 1 °C from year 2000 to 2100. For as far as we know now, this is an unrealistic prediction for the coming century but we incorporated it as an absolute minimal change to compare with the more likely scenarios of a 2 °C and 4 °C temperature increase by 2100 (HadleyCentre 2003). When translating these scenarios to temperature isocline speeds we assumed that the simulated metapopulation was situated along the European Atlantic coast. Unaffected by mountain ranges it has the temperature gradient of 0.0042 °C per km (Schippers *et al.* 2011). The three scenarios were therefore equivalent to isocline speeds of respectively 2, 4 and 8 km per year. Weather variability was modelled as the standard deviation of the average temperature, which currently is 0.59 °C and was thus translated to 140 km (Schippers *et al.* 2011). To assess the effect of increased weather variability we also applied levels of 280 km and 0 km.

At initialisation of the model, all habitat patches were filled with 10 adult individuals, equaling half the carrying capacity. Each individual was randomly given 2 alleles per locus for 10 different, unlinked loci. The initial alleles had allele numbers ranging from 1 to 20. We allowed for mutations at a rate of 10^{-4} per generation, the mutation rate of medium-sized (20 repeats) microsatellites per haplotype per generation (e.g. Whittaker *et al.* 2003). Mutations generated new alleles with a random number between 21 and 50 (for more detailed information see Appendix 2.2: Genetic make-up and protocol). All alleles were neutral and thus had no effect on individual performance.

After initialisation we allowed a generous burn-in of 3000 generations to obtain the equilibrium situation (for more detailed information see Appendix 2.2). During these 3000 generations, the model was run with temperature zone speed equaling zero but the simulated weather variability was already used. In the remainder of the paper, time 0 was set after the burn-in.

Schippers *et al.* (2011) found that under the parameter settings used, this species responded differently to our three different temperature zone shift scenarios. This allowed us to study the genetic signatures of three demographically different range shifts: no decline in population numbers, slow decline and fast decline.

Simulation experiments

With our first experiment we investigated how predicted temperature increase affected the level and distribution of neutral genetic diversity in the species range in time. In this experiment the temperature isoclines were simulated to move northward for 600 years according to the three climate scenario speeds and one control speed of zero km per year. The weather variability was maintained at the estimated current value of 140 km throughout the entire experiment.

With our second experiment we investigated the combined effect of both predicted temperature increase and increased weather variability on the level and distribution of neutral genetic diversity in the species range in time. In this experiment the temperature isoclines were again simulated to move northward for 600 years according to the three climate scenario speeds and one control speed of 0 km per year, but now for each of these scenarios the weather variability had values of 0, 140 or 280 km.

Analysis

For both experiments we were interested in the changes in level and distribution of neutral genetic diversity in time and space. We calculated two measures of genetic diversity: the average actual number of alleles per locus (A) and the average effective number of alleles per locus (A_e), with the latter following the equation (Frankham *et al.* 2005):

$$A_e = \frac{1}{\sum_i p_i^2},$$

where p_i denotes the frequency of allele i in the population. Field studies take samples of the entire population and are thus confined to using A_e . Differences between A and A_e provide information about low-frequency alleles, such as new mutations. We stored and analysed data for 13 time slices consisting of the years: 0, 25, 50, 75, 100, 125, 150, 200, 250, 300, 400, 500, and 600. To investigate the distribution of genetic diversity we cut the landscape in ranges of 50 km and calculated A and A_e both for the whole metapopulation and for the combined populations in each 50 km range. To study the distribution of genetic diversity within these 50 km ranges, we furthermore calculated the genetic differentiation between populations (F_{ST}) for the combined populations in each range. Lastly, to compare with and correct for population size, we calculated the average number of individuals (N). For structuring the data and calculating the allele frequencies and F_{ST} values we used Genepop 4.0 (Rousset 2008).

For studying trends in numbers of individuals and alleles, we averaged these per parameter setting. For individuals we averaged over the two runs of the five landscape variants, for alleles we also averaged over the 10 loci. For both experiments we calculated confidence intervals to show variation between different runs.

RESULTS

The effects of predicted temperature increase: level of neutral genetic diversity

The first experiment showed that under the temperature isocline speed of 0 and 2 km per year, the number of individuals in the metapopulation remained more or less the same over a period of 600 years (Figure 2.1a). Under speeds of 4 and 8 kilometers per year, individual numbers linearly decreased after a small lag phase, which ended in the metapopulation going extinct under the conditions simulated in these scenarios. The decrease in number of individuals was correlated with temperature isocline speed, i.e., the faster the temperature optimum moved, the faster the number of individuals decreased and the sooner extinction occurred.

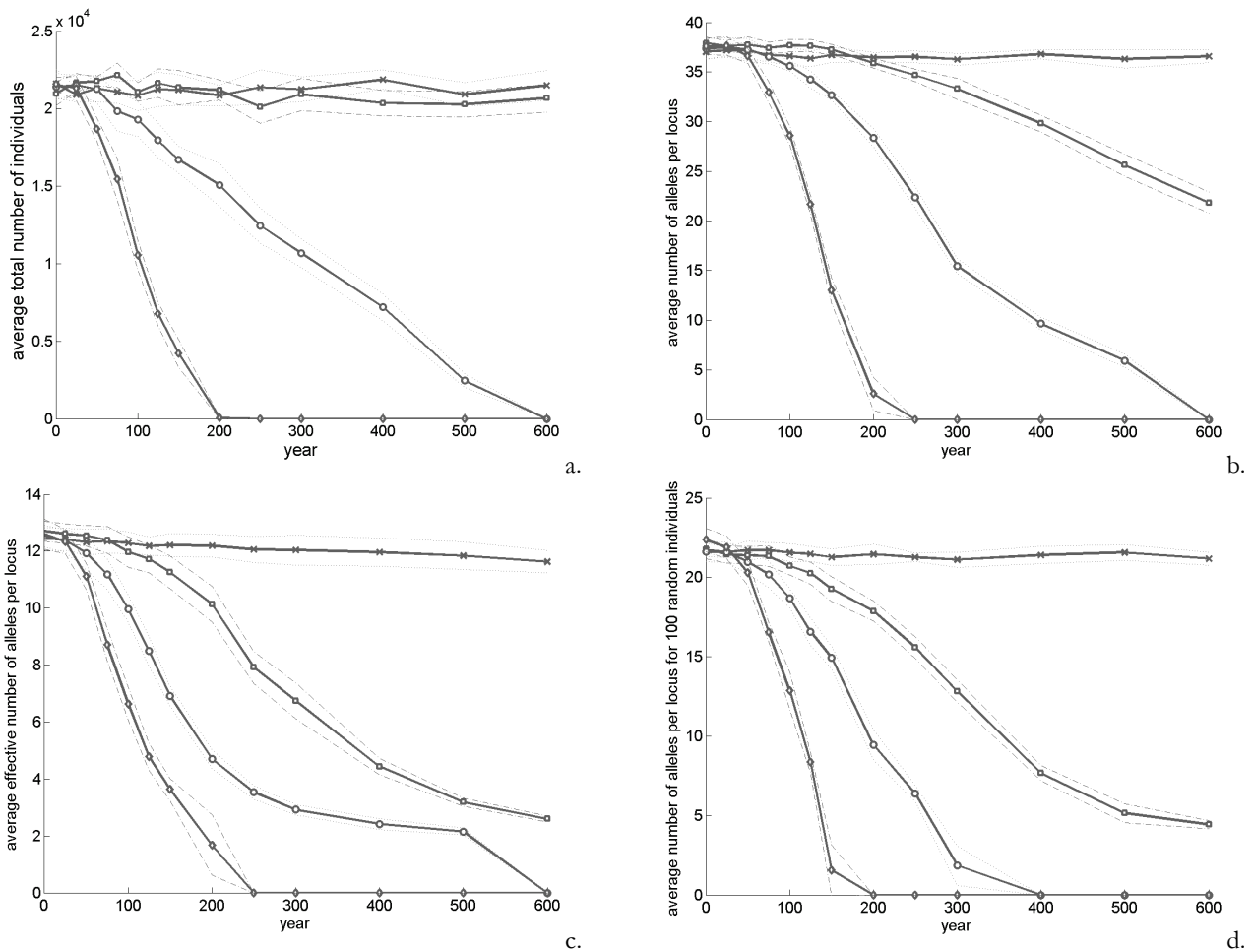


Figure 2.1. The effects of four temperature isocline speeds 0 (x), 2 (□), 4 (○), and 8 (◇) km per year on average number of individuals (a), average number of alleles per locus (b), average effective number of alleles per locus (c), and average number of alleles per locus for 100 random individuals (d). Dotted lines (.. and -.) give 95% confidence intervals. Fig. b-d: Data are the average of 10 loci. Weather variability was 140 km.

The average number of alleles per locus showed a somewhat different result (Figure 2.1b). The number of alleles decreased in time in all climatic change scenarios, including the 2 km per year temperature isocline shift scenario in which the number of individuals did not decrease. The decline of the number of alleles was faster with increased temperature isocline shift speed. The average effective number of alleles per locus also decreased in time in all scenarios at a rate negatively correlated to the speed of the temperature isocline shift (Figure 2.1c). However, the rates of decline were higher than

those of the average number of alleles under the same scenario. The loss of alleles could in part be the result of the decreasing population size (but notice the 2 km per year scenario). To correct for this potential effect we selected a subset of 100 individuals for all scenarios and time slices. Also in such a sample of constant population size, alleles were lost in all scenarios (Figure 2.1d). The effective numbers of alleles showed the same pattern (not shown).

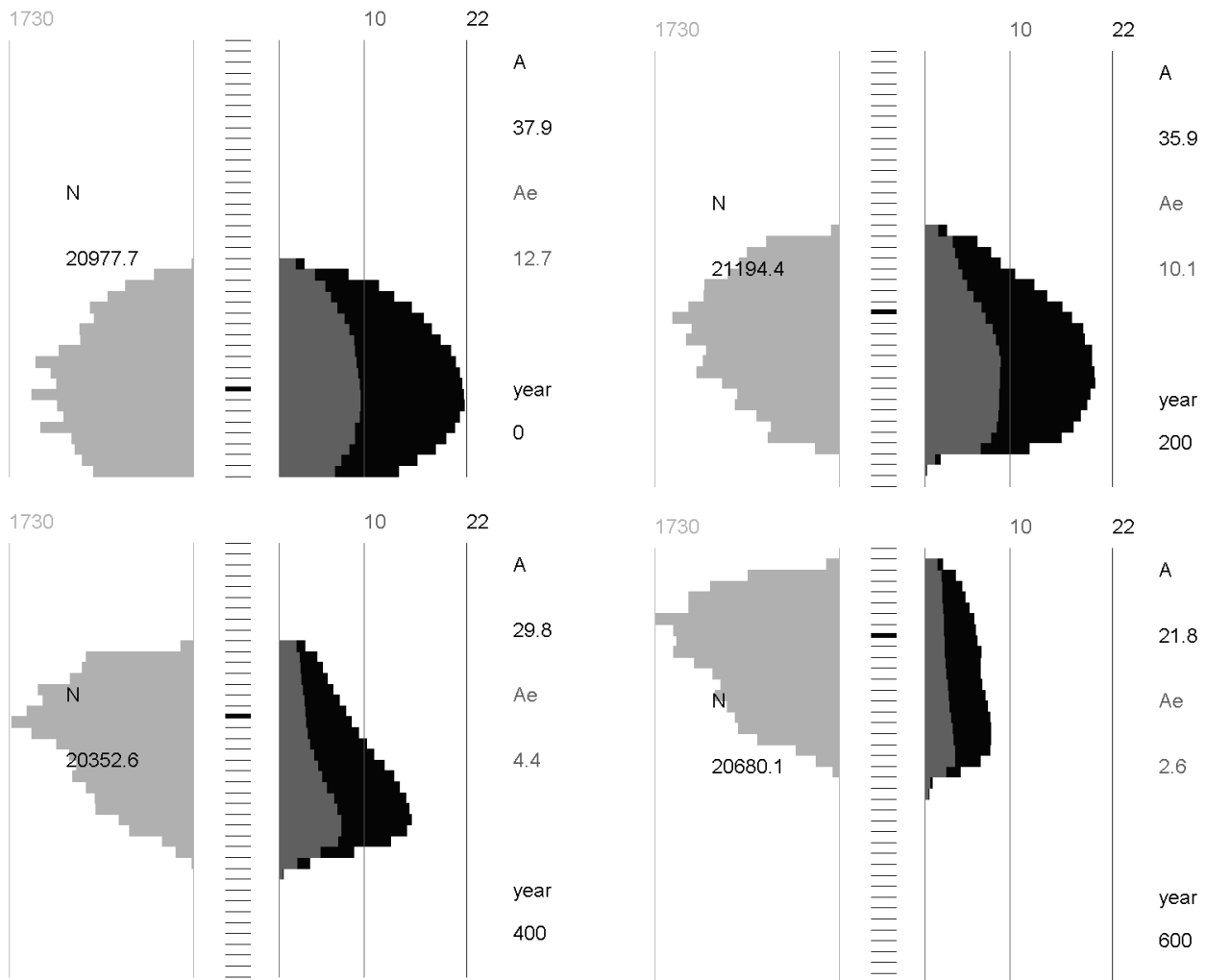


Figure 2.2 The spatial distribution of individuals, alleles and effective number of alleles during the movement of the habitat optimum northwards at 2 km per year, in 4 time steps: year 0, 200, 400 and 600. For assessing the number of individuals and their neutral genetic diversity the populations were grouped in 50 km ranges, displayed as the horizontal lines in the figure center. The bold horizontal line indicates the year-specific location of the temperature optimum. The bars display the average number of individuals per 50 km range (light gray, to the left), and the number of alleles (in black, to the right) and effective number of alleles (in dark gray, to the right). In each time slice (year indicated at the bottom right) also the total number of individuals (N), alleles (A) and effective number of alleles (A_e) for the whole metapopulation are indicated. The vertical lines serve as scales and specifically indicate the found maximum numbers of individuals and alleles in any 50 km range across all time slices. Weather variability was 140 km.

The effects of predicted temperature increase: spatial distribution of neutral genetic diversity

Figure 2.2 displays for one temperature increase scenario (the 2 km per year temperature isocline shift) the spatial distributions of individuals, alleles and effective number of alleles during the movement of the climate optimum northwards. The peak of the distribution of individuals more or less followed the temperature optimum during its movement northward, but the individuals that occupied the newly

colonized area north of the original habitat carried only a small subset of the alleles. Most of the alleles present in populations that used to be in the centre of the metapopulation prior to temperature change, remained there. This led to a highly skewed distribution of the –effective– number of alleles in the metapopulation from year 250 onwards, with populations towards the trailing edge of the metapopulation being significantly more genetically diverse. As the climate optimum continued to move northward, these populations started to decrease in size and finally went extinct, leading to loss of alleles.

Figure 2.3 shows the distribution of the F_{ST} values of all 10 simulated runs within each 50 km range for the 2 km per year temperature isocline shift. Most F_{ST} values were very small, but there was a tendency towards higher values near the range edges, where the average numbers of individuals were lower (compare Figure 2.2 with Figure 2.3). The F_{ST} values in scenarios of 4 and 8 km per year temperature isocline shift showed similar patterns (not shown).

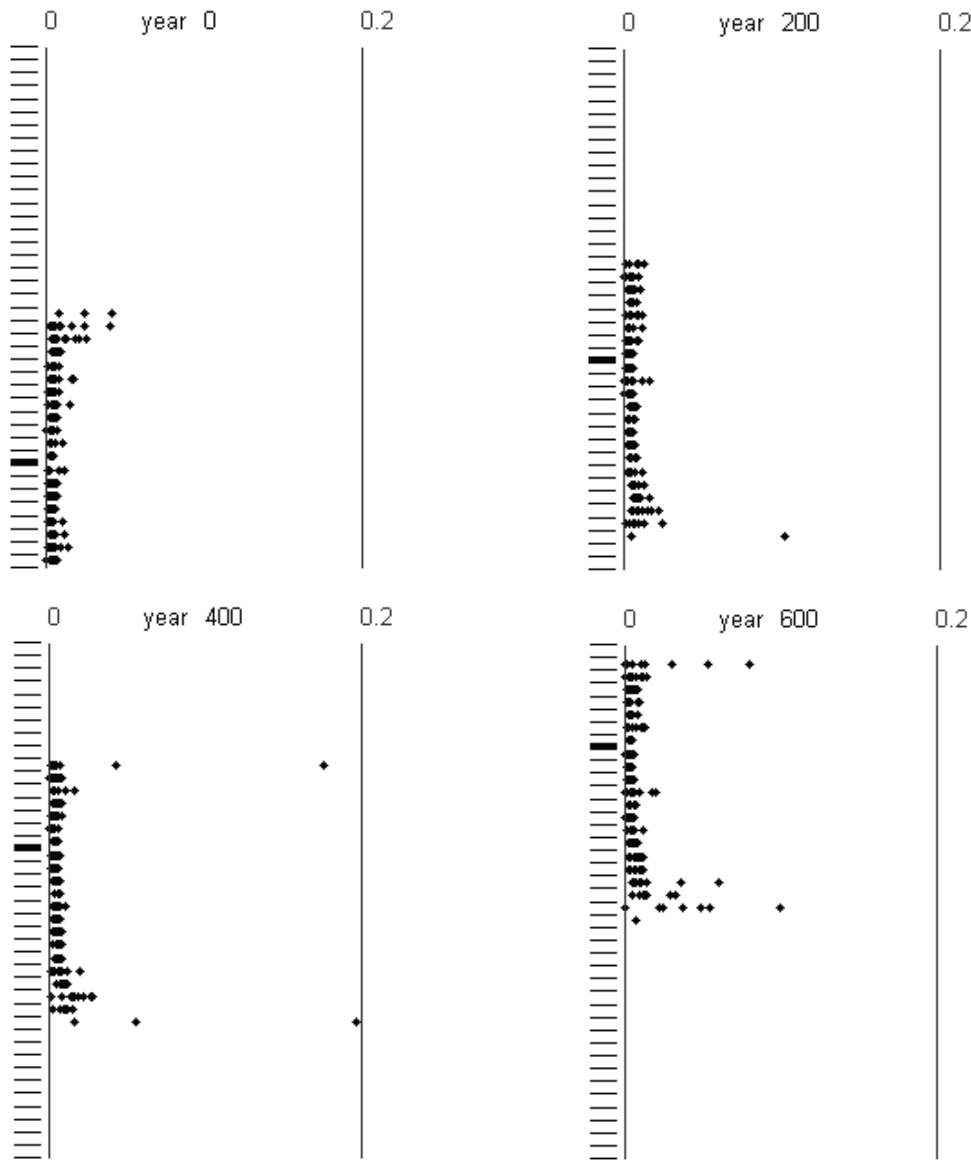


Figure 2.3. All F_{ST} values in each 50 km range (displayed as the horizontal lines in the figure center) during the movement of the temperature optimum (bold horizontal line) northwards at 2 km per year. Missing values (i.e. less than 10 F_{ST} values noted per range) are the result of simulations leading to 0 individuals in this range. Weather variability was 140 km.

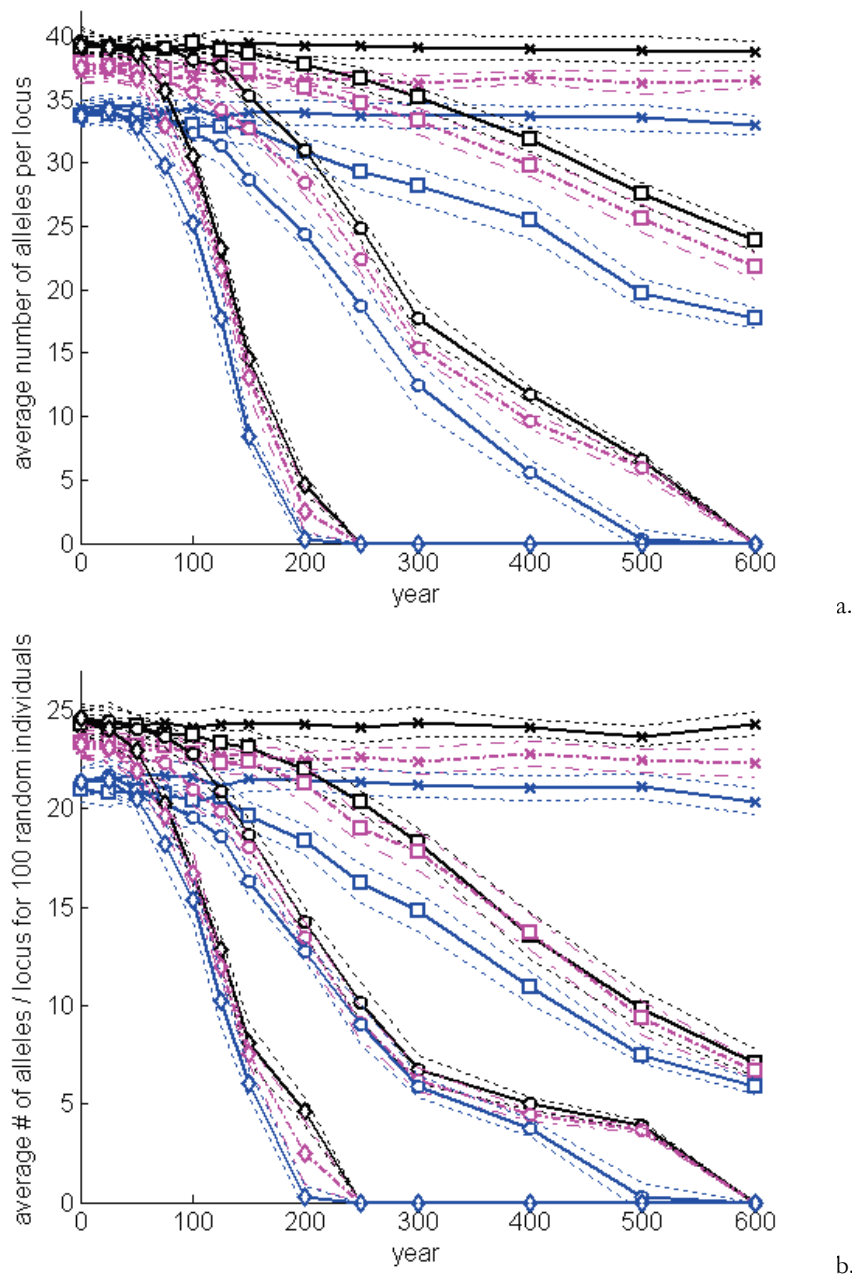


Figure 2.4. Average number of alleles per locus per year (a) and average number of alleles per locus for 100 random individuals per year (b) for all combined temperature isocline speeds 0 (—x—), 2 (—□—), 4 (—○—), and 8 (—◇—) km per year, and random weather variabilities of 0 (black), 140 (magenta) and 280 (blue) km. Dotted lines indicate confidence intervals.

The interaction of predicted temperature increase and increased weather variability: level of neutral genetic diversity

We ran our temperature change scenarios at twice the standard level of random weather variability, so with a standard deviation (SD) of the temperature optimum of 280 km, and for comparison also without any random weather variability between years (SD=0). The results indicated two different effects of an increase of weather variability. Firstly, the number of individuals (see Fig. 2.7a in Appendix 2.3: Extra figures) and the actual (Fig. 2.4a) and effective numbers of alleles (see Fig. 2.7b in Appendix 2.3) were smaller under larger weather variation across the whole range. This is already visible at $t=0$, as the weather variability was already simulated during the burn-in phase. Corrected for

the decrease in population size (Fig. 2.4b), we see that increased weather variability led to a small loss of neutral genetic diversity independent of population size. Secondly, the variation in the number of individuals between replicate runs was larger under increased weather variability (see Fig. 2.7a in Appendix 2.3: Extra figures). Increasing variation is indicated by increasingly wide confidence intervals with increasing weather variability.

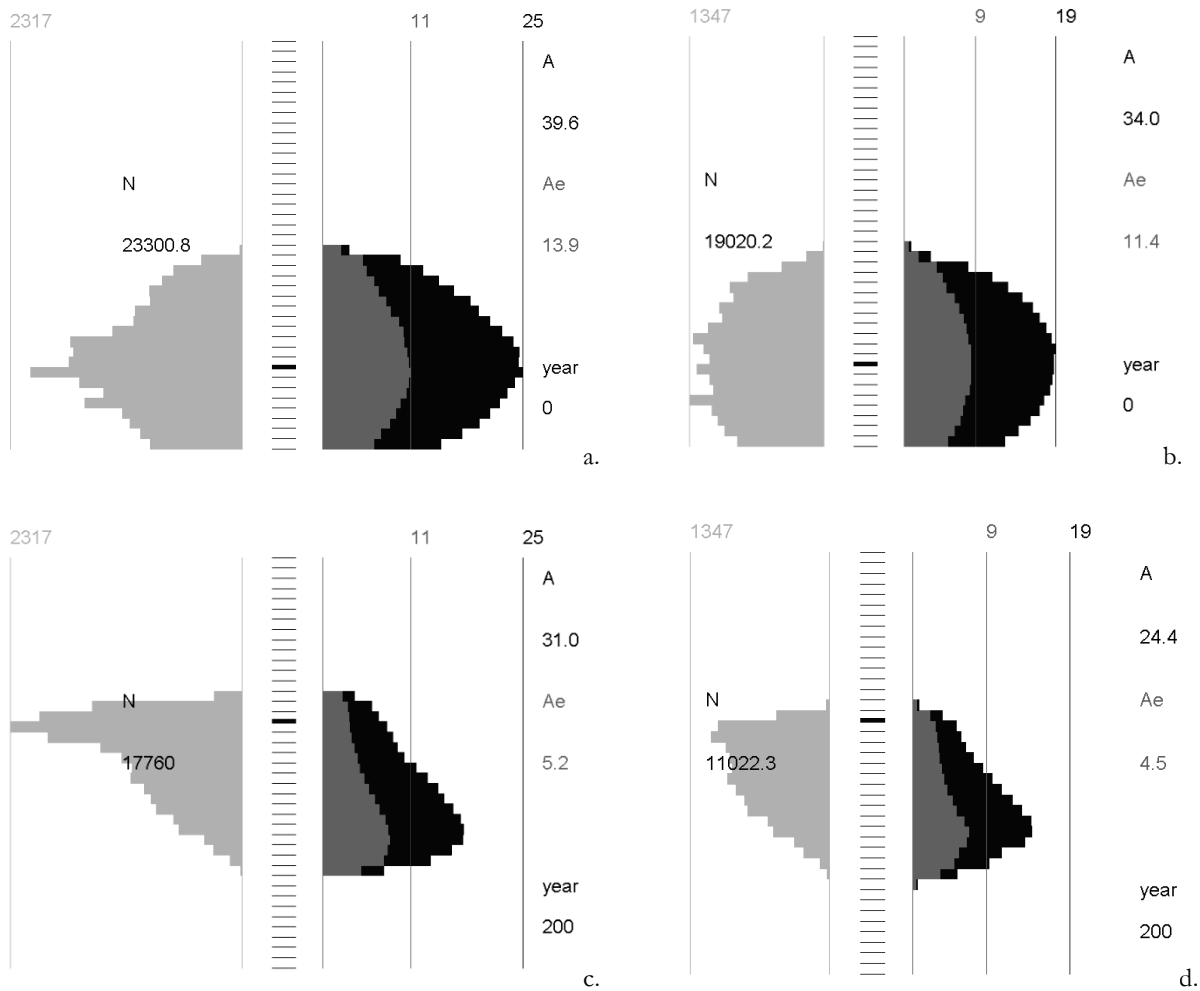


Figure 2.5. Overview of differences in spatial distribution of individuals, number of alleles per locus and effective number of alleles per locus in each 50 km range (displayed as the horizontal lines in the figure center) at 4 km per year optimum temperature (bold horizontal line) speed for random weather variabilities of 0 (a, c) and 280 (b, d) km in years 0 (a, b) and 200 (c, d). The bars display the average number of individuals per 50 km range (light gray, to the left), and the number of alleles (in black, to the right) and effective number of alleles (in dark gray, to the right). In each time slice (year indicated at the bottom right) also the total number of individuals (N), alleles (A) and effective number of alleles (A_e) for the whole metapopulation are indicated. The vertical lines serve as scales and specifically indicate the found maximum numbers of individuals and alleles in any 50 km range in all time slices of a single averaged parameter set.

The interaction of predicted temperature increase and increased weather variability: Spatial distribution of neutral genetic diversity

The increase in weather variability did not affect the initial metapopulation range (compare fig. 2.5a and 2.5b as typical examples of what we see under all scenarios), nor did it affect the retraction of the rear end of the species range (compare Fig 2.5c with 2.5d). However, the peak distribution of individuals was flattened under large weather variability, which is the main reason why the metapopulation contained fewer individuals under larger weather variability. Apparently, a large yearly variation

prevented the species from fully occupying the habitat under optimal conditions, leading to increased habitat occupancy under limited weather variability. Under temperature increase, the overall pattern of individual and allele distributions under range shifts was however not affected by increased weather variability, despite the effect on absolute numbers (compare 2.5a with 2.5c, and 2.5b with 2.5d).

In Figure 2.6 we show the distribution of the F_{ST} values of all 10 simulated runs within each 50 km range for the scenario of 4 km per year temperature isocline shift under weather variabilities of zero and 280 km. Range edges again showed a tendency towards higher F_{ST} values. Besides this effect, there was more variation in the F_{ST} values throughout the entire metapopulation under high weather variability. This last effect was independent of local population sizes.

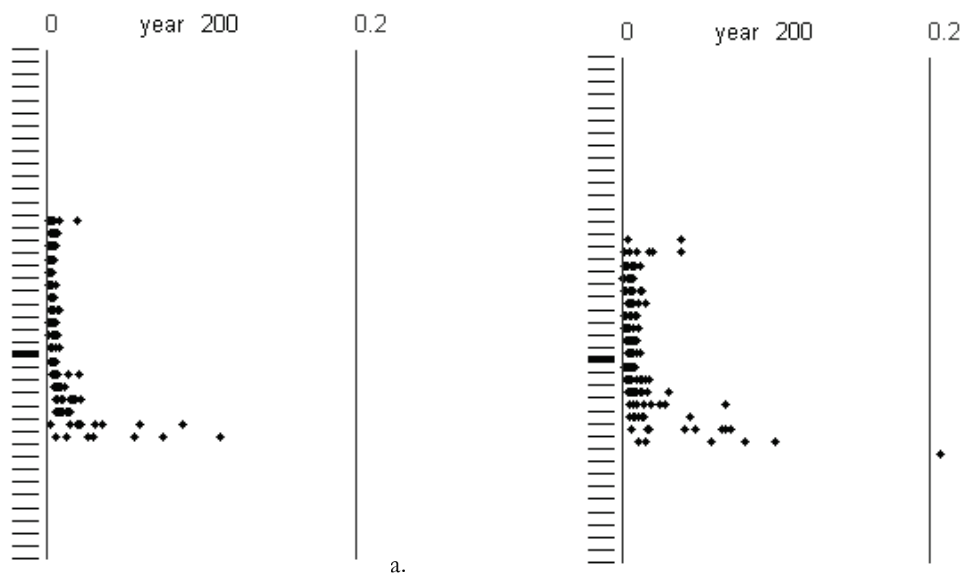


Figure 2.6. All F_{ST} values in each 50 km range (displayed as the horizontal lines in the figure center) during the movement of the temperature optimum (bold horizontal line) northwards at 4 km per year in time slice year 200, under weather variabilities 0 (a) and 280 (b). Missing values (i.e. less than 10 F_{ST} values noted per range) are the result of simulations leading to 0 individuals in this range.

DISCUSSION

The purpose of this study was to investigate how range shifts induced by the predicted climate change may affect the level and distribution of neutral genetic diversity in a species range. For this we modelled both demography and genetics of a species with medium dispersal capacity in a metapopulation setting under climate-induced range shifts. Range shifts induced by the predicted temperature increase led to loss of neutral genetic diversity in the metapopulation, even if the metapopulation size remained unaffected. When comparing the effects of temperature increase and weather variability in our model, temperature increase appeared to be the dominant factor in affecting population size, the level of neutral genetic diversity and the spatial distributions of both. The genetic differentiation between populations increased due to increased weather variability and in range margins, but this effect was limited.

Effects of range expansions and range shifts on population genetics have been studied before (e.g. Edmonds *et al.* 2004, Excoffier *et al.* 2009, Hewitt 1996, Klopstein *et al.* 2006, McInerny *et al.* 2009, Travis *et al.* 2007). With this study we have attempted to make a species-specific assessment of the

effect of climate change on neutral genetic diversity. For this we incorporated, in contrast to similar modelling studies, species-specific life history traits, diploid inheritance of alleles, temperature variability and predicted increase of temperature, and spatial irregularity through random habitat configurations. Thus we could study simultaneously how metapopulation demography was affected by climate change and in turn affected the metapopulation genetics for a specific species.

The results of this study provide insight into how projections of current climate change may affect metapopulation-wide neutral genetic diversity in dispersers of medium quality. Besides, the results illustrate the usefulness of more realistic models for studying these complex issues. Further, we hope this study may provide additional food for thought in assessments of currently used monitoring tools and conservation programmes.

The effects of temperature increase induced range shifts on neutral genetic diversity

Neutral genetic diversity was lost under all three temperature increase scenarios, and this loss also occurred when the number of individuals did not decrease during range shift, which was only the case in the 1° C temperature increase per century scenario. The loss of neutral genetic diversity was visible both as a decrease of the actual number of alleles (the sum of common and (very) rare alleles) and of the effective number of alleles (which corrects for differences in allele frequencies). It was also present when we corrected for differences in population size. Schippers *et al.* (2011) concluded that metapopulation survival can be enhanced by limiting future temperature increase. We subscribe to this conclusion and extend it to the preservation of neutral genetic diversity. However, in our model all range shifts led to loss of neutral genetic diversity, suggesting that some loss of genetic diversity may be inevitable under a broad range of scenarios of climate change.

Neutral genetic diversity was lost as a result of a series of effects. The genetic diversity near the ranges of the metapopulation was lower than in the centre as a result of lower habitat suitability, and thus lower population density (Eckert *et al.* 2008). Besides, the genetic diversity of individuals dispersing into newly suitable areas was only a part of the gene pool present near the original leading range. As a result, populations in newly colonised habitats at the leading edge of the metapopulation only contained a fraction of the neutral genetic diversity that was present in the centre of the metapopulation. Earlier studies (Edmonds *et al.* 2004, Excoffier & Ray 2008, Klopstein *et al.* 2006) have shown low-frequency alleles at the leading range edge to reach high frequencies in newly colonised areas, at the cost of the presence and abundance of other alleles. This is called the surfing effect. Travis *et al.* (2007) in a study on adaptive mutations, showed that this effect is strong enough to even increase the frequencies of deleterious mutations in new populations. In other words, selection may not undo the demographic effect of serial founder events, as was predicted by Nei (1975). Here we show that the same mechanism leads to the loss of existing neutral alleles in a metapopulation. The total number of alleles was lower in newly colonized areas, indicating that not all alleles entered the new habitat. The effective number of alleles declined faster than the actual number of alleles, most clearly in the 1° C and 2° C temperature increase per century scenarios, indicating that a few alleles increased in frequency at the expense of the abundances of all other alleles. This result is consistent with previous work on mutations (Edmonds *et*

al. 2004, Klopstein *et al.* 2006, Travis *et al.* 2007) which showed that a low initial frequency does not prevent an allele from surfing.

As the metapopulation continued to move in time, the consequence of this surfing behaviour was that the patches with the highest level of allelic diversity, which were originally at the centre of the metapopulation, became situated in the lagging edge in the southern range. This has been shown before in a strategic model of the fate of neutral markers (McInerny *et al.* 2009). On a different scale of space and time, it resembles the distribution of neutral genetic diversity in diverse groups of species which have undergone range expansion across central and northwestern Europe after the last ice age (Besold *et al.* 2008, Hewitt 1996). Hampe & Petit (2005) have pointed out the relative importance of rear-edge populations as long term stores of species' genetic diversity. In our model, the location of the maximum genetic diversity was more or less stationary in space, but the metapopulation as a whole shifted northward. This was not the consequence of an inability of alleles to move within the metapopulation but of a slow effective rate of movement. Boileau *et al.* (1992) already showed persistent founder effects in natural populations. They concluded from theory and computer simulations that allele frequencies established during colonisation by few individuals are resistant to decay by allele exchange, when this population grows rapidly after founding.

Finally, when southern populations started to go extinct once temperature became too high in that region, neutral genetic diversity was lost. This process leading to allele loss concurs with theory (Nei *et al.* 1975), strategic modelling studies (Boileau *et al.* 1992, McInerny *et al.* 2009) and empirical findings (Boileau *et al.* 1992, Hewitt 1996).

One would expect that the loss of neutral genetic diversity is aggravated under decreased population connectivity. However, we used model parameters for the species and for the landscape that together produced a well-connected metapopulation, with F_{ST} values calculated for the whole stationary metapopulation ranging from 0.0475 to 0.0868 under average weather variability. Thus there is no reason to assume that limited population connectivity was causing the loss of neutral genetic diversity we observed. We did find an increased number of instances of higher genetic differentiation between populations near range margins (as shown by Eckert *et al.* 2008). This was probably related to the smaller average population sizes in these margins. However, even in marginal regions F_{ST} values only occasionally went up to 0.2, and decreased again when population sizes increased in the newly colonised areas. Thus in our model colonisation had no long-term effect on genetic differentiation among patches. This pattern was observed for all temperature increase scenarios.

The landscapes we used in our model were 15 x 2000 km. One may expect that the loss of neutral genetic diversity is more pronounced in linear habitats where dispersal follows a stepping stone model. However, in our landscapes the east and west side were merged to diminish edge effects, which in theory leads to an infinitely wide landscape. In metapopulation simulations this is fairly common practice, see e.g. Johst *et al.* (2002). With 3000 patches of 400 meters radii, there were always several locations available for dispersing individuals directly north of the northern metapopulation edge. The cylindric structure of the landscape does increase population connectivity compared to what can be expected in a wider, flat, or real-life landscape with the same properties, as individuals can reach a new habitat patch along different routes in east-west direction (Hovestadt & Poethke 2005). This may

contribute to the low F_{ST} values that we found. However, Beaumont and Nichols (1996) also performed their simulations on a torus while studying effects on F_{ST} values. Besides, this effect was small compared to the benefit of avoiding edge effects. In addition, it contributed to a less stochastic behavior of the colonisation process at the leading edge, which simplified the interpretation of the results. Real species distribution areas will often contain stretches in which suitable habitat is confined to a few patches in a narrow corridor, and such bottlenecks can be expected to lead to an even more pronounced loss of neutral genetic diversity under range shifts than we have shown here under unconstrained dispersal.

We used current climate change scenarios (2° and 4° C warming by 2100) and projected them over the next 600 years. It is unlikely that current projections will be valid for such a long time period. It is relevant, however, that if we would be able to stop temperature increase by for example 2100, the modelled metapopulations will not yet have gone extinct under both temperature increase scenarios, and they will still contain most of their genetic diversity in the surviving southern original parts of their ranges.

The effects of increased weather variability on neutral genetic diversity under range shifts

We found that neutral genetic diversity was always lowest under high weather variability, independent of population sizes. Under high weather variability, population sizes at climate optimum did not reach carrying capacity. As a result genetic drift in these populations increased compared to scenarios with lower weather variabilities, leading to lowered levels of neutral genetic diversity in these populations and thus overall in the metapopulation. Although differences between weather variability scenarios were small and arguably negligible compared to the effects of temperature increase, we did see that these initial differences in neutral genetic diversity were maintained throughout the time series. The effect of weather variability on level of neutral genetic diversity was therefore small yet persistent. There was also a small increase in the occurrence of higher genetic differentiation between populations throughout the metapopulation under increased weather variability, probably also the result of an increase in genetic drift.

In our study the simulated weather variability was already implemented during the burn-in phase of the model run, and we did not study the effect of an increase in weather variability at the start of the climate change scenarios. However, the differences between the average weather variability and the two extreme values of no and twice as much weather variability were so much smaller than the temperature change effects that they probably would have gone unnoticed if they had occurred together.

Perspectives

Until now, weather variability has not often been taken into account separately in climate change studies (but see e.g. Schippers *et al.* 2011, Verboom *et al.* 2010). Verboom *et al.* (2010) concluded that increased weather variability can have important consequences for species' conservation programmes. Our results may be taken to suggest that the effect of weather variability is small with regard to the loss of genetic diversity caused by temperature change. However, as in our model the climate suitability follows a stable, yet moving, curve throughout the simulated time series, the random effects on

temperature optimum are always spatially correlated: if temperature is not optimal at a given location in a certain year, there will be always be optimal conditions further to the north or to the south. So there is never a threat to the whole metapopulation simultaneously. This is not representative of extreme weather events such as the hot summer of 2003, when there were very high temperatures all over Europe. It would thus be interesting to study the effects of weather variability on population sizes and genetic diversity in metapopulations more thoroughly and with methods different from ours.

Our model did not include rare long distance dispersal, which might support metapopulation survival or improve migration under climate change. However, in contrast to plants, our model species requires a mate to reproduce, and this could seriously hamper successful colonization by the occasional long distance migrating bird. Furthermore, rare long distance dispersal that is successful would likely aggravate the founder effects shown in this study.

Another contribution to survival beyond our model predictions could come from selection and adaptation to changing conditions, rather than (or combined with) merely following the conditions that are currently optimal. Outbreeding, long-lived species such as trees maintain most of the genetic variation within a population (Austerlitz *et al.* 2000), and selection takes place every generation (Savolainen *et al.* 2007). Whether bird species in fragmented landscapes may be able to do the same is unclear. However, if adaptation occurs, it may be at the expense of part of the genetic diversity, which is selected against or lost together with increased selection.

In small patches with low genetic diversity, inbreeding may have an adverse effect on population demography, through e.g. a decreased number of offspring, in species that are sensitive for inbreeding. We did not include inbreeding in our model, as we were interested in demographic effects only. Besides, we modelled a medium disperser in a reasonably connected landscape. In such a landscape inbreeding can be effectively avoided by dispersal (Szulkin & Sheldon 2008).

Current biodiversity monitoring systems usually assess the number of individuals at regular intervals, and the IUCN red lists of endangered species categories are based on assessments of population sizes, the level of fragmentation and the span of occurrence, in combination with species traits. Our results, supported by earlier empirical studies (Hewitt 1996, Neve *et al.* 2009), indicate that these biodiversity monitoring tools may not accurately reflect the trend in level of species' genetic diversity. Laikre *et al.* (2010) state that currently used indicators focusing on genetic diversity only deal with breeds used for food production. Laikre *et al.* (2008) suggested starting points for a genetic diversity monitoring program, but they did not take effects of climate change into account in their study.

From this and previous studies it can be concluded that species experiencing climate-induced range shifts may be prone to loss of genetic diversity. More research is needed to develop good indicators of monitoring genetic diversity in species subject to climate change-induced range shifts and, more importantly, to develop conservation programmes and management tools to prevent such losses (Smulders *et al.* 2009). However, initially most of the genetic diversity may still be available in populations in the original species range centre. Our results indicate the importance of conserving such areas as modern refugia of genetic diversity, as argued earlier by Hampe and Petit (2005).

APPENDIX 2.1: DETAILED MODEL DESCRIPTION

For this study we used METAPHOR, a simulation model for metapopulation demography (Verboom *et al.* 2001, Vos *et al.* 2001b). The model has been extended to allow for stochastic temperature zone shifts by Schippers *et al.* (2011). Here a new extension provided each individual in this study with a genome of 10 unlinked diploid genes (for more detailed information see Appendix 2.2: Genetic make-up and protocol).

Neutral population genetics in our model is the result of population demography. There is no reciprocal effect of genetics on demography. The yearly metapopulation demography is simulated based on four events: reproduction, dispersal, survival and aging, in this order. Reproduction, dispersal and survival are based on population density and habitat quality. Habitat quality is controlled by time and location specific temperature. As such we simulate the effect of stochastic temperature zone shifts on neutral genetic diversity.

Landscape

The landscape we used in the model had dimensions of 15 km from east to west by 2000 km from north to south. The east and west side were merged to create a cylindric landscape. The landscape contained 3000 circular habitat patches of 50 ha each, so consisted of a total of 5% habitat. When generating the landscape, patches were placed in random positions in the landscape, yet only allowed if they were at a minimum distance of 150 m from existing patches. Five landscape variants with different habitat positions were randomly generated in this way.

Species

We modelled a woodland bird, parameterised as the middle spotted woodpecker (*Dendrocopus medius*). Parameters were based on biological information (Hagemeijer & Blair 1997, Kosenko & Kaigorodova 2001, Kosinski *et al.* 2004, Kosinski & Ksit 2006, Michalek & Winkler 2001, Pasinelli 2000, Pettersson 1985a, Pettersson 1985b) and on the interpretation by Schippers *et al.* (2011) (see Table 2.1). The model distinguishes 2 sexes and 2 lifestages: adults and juveniles. The yearly life cycle consists of recruitment, dispersal, and survival, in this order. Lastly, all juveniles age to adults. Recruitment, dispersal and survival are all dependent of life stage, population density (PD) and habitat quality (HQ).

$$PD = N_i / CC,$$

with N_i : number of individuals in patch,

CC : carrying capacity of patch, and

HQ : see section Climate in this appendix.

Species: recruitment function

The number of nests in a patch in each generation is equal to the number of unique adult pairs of opposite sex in this patch, with a maximum of 10. The number of offspring per nest is then found with:

$$N_O = N_{O_PD_0HQ_1} * \left(1 - \left(1 - \frac{N_{O_PD_0HQ_0}}{N_{O_PD_0HQ_1}} \right) * (1 - HQ) \right) * \left(1 - \left(1 - \frac{N_{O_PD_1HQ_1}}{N_{O_PD_0HQ_1}} \right) * PD \right)$$

with $N_{O_PD_0HQ_1}$: number of offspring at population density (PD) = 0 and habitat quality (HQ) = 1, and similar for $N_{O_PD_0HQ_0}$ and $N_{O_PD_1HQ_1}$. See Table 2.1.

Species: survival function

Determines for each individual the chance that it survives the current year, P_S .

$$P_S = P_{S_PD_0HQ_1} * \left(1 - \left(1 - \frac{P_{S_PD_0HQ_0}}{P_{S_PD_0HQ_1}} \right) * HQ \right) * \left(1 - \left(1 - \frac{P_{S_PD_1HQ_1}}{P_{S_PD_0HQ_1}} \right) * (1 - PD) \right)$$

with $P_{S_PD_0HQ_1}$: survival rate at population density (PD) = 0 and habitat quality (HQ) = 1, and similar for $P_{S_PD_0HQ_0}$ and $P_{S_PD_1HQ_1}$. See Table 2.1.

Species: dispersal function

Determines for each individual the yearly chance that it leaves its patch to go on dispersal, P_D .

$$P_D = P_{D_PD_0HQ_1} * \left(1 - \left(1 - \frac{P_{D_PD_0HQ_0}}{P_{D_PD_0HQ_1}} \right) * HQ \right) * \left(1 - \left(1 - \frac{P_{D_PD_1HQ_1}}{P_{D_PD_0HQ_1}} \right) * (1 - PD) \right)$$

with $P_{D_PD_1HQ_1}$: dispersal rate at population density (PD) = 1 and habitat quality (HQ) = 1, and similar for $P_{D_PD_1HQ_0}$ and $P_{D_PD_0HQ_1}$. See Table 2.1.

If an individual disperses, we need to determine where it goes. From their origin patch individuals can go in every direction, along a straight line. Connectivity to other patches is determined by destination patch radius (r) and distance to there (d). So the chance to disperse from patch A to patch B is:

$$P_{AB} = \frac{2 * \arcsin\left(\frac{r_B + l}{d_{AB}}\right)}{2\pi}$$

with l is 150 m, the maximum distance from where an individual can detect suitable habitat. The maximum dispersal distance is 15 km, so habitat patches that are separated by more than this distance are not connected at all. Our model does not allow dispersers to ignore a nearer patch, so more distant patches are located in the shadow of the nearer patch. An individual may arrive in a patch with a population size larger than carrying capacity twice per dispersal event, and is then allowed to disperse again. Should it fail to reach a habitable patch within a total of three dispersal rounds, it dies.

Climate

Climate is incorporated in the model through habitat quality. Where climate is optimal for the species, habitat quality equals 1, and where climate is unsuitable for the species, habitat quality is 0 (see equation HQ below). Climate change scenarios are based on temperature increase predictions (I °C year⁻¹) by the Hadley Centre of 0.0167 and 0.0333 °C year⁻¹, and we also included a scenario with a temperature increase of 0.084 °C year⁻¹. Besides, the used scenarios include weather variability increase assumptions as temporal stochasticity in the temperature (the current standard deviation of the average temperature σ_t (°C), 0.59 °C (Schippers *et al.* 2011). Climate in our model is thus defined as the temperature in year t and at location Y . Climate change is then the speed with which temperature isoclines travel north (T km year⁻¹) and the yearly fluctuation of these lines (σ_d km). We use a climatic gradient from south to north of G (°C km⁻¹) to get to:

$$T = I / G, \text{ and}$$

$$\sigma_d = \sigma_t / G$$

This results in a current yearly fluctuation of the temperature isoclines σ_d of 140 km, and we further included scenarios with yearly fluctuations σ_d of 0 km and 280 km. We can then calculate the location of the optimal temperature in north-south direction (Y_{opt}) in a certain year as:

$$Y_{opt,t} = Y_{opt,0} + T * t + \sigma_d * N_t$$

with N_t is the yearly random number drawn from a standard normal distribution.

We obtain a normal habitat quality distribution with this optimal coordinate Y_{opt} in its centre by defining habitat quality (HQ) as

$$HQ_{patch,t} = \exp \left[\frac{-0.695(Y_{opt,t} - Y_{patch})^2}{H^2} \right]$$

H is an indicator of the temperature tolerance of the species, and defined as the distance from the temperature optimum at which habitat quality is 0.5. See Table 2.1.

Initialisation

At initialisation of the model, all habitat patches were filled with 10 adult individuals, equaling half the carrying capacity. Each individual was randomly given 2 alleles per locus for 10 different, unlinked loci (for more detailed information see Appendix 2.2: Genetic make-up and protocol). The climate optimum Y_{opt} was initialised at 400 km from the southern landscape edge.

Burn-in

After initialisation the model was run for 3000 generations, thus 3000 years (for more detailed information see Appendix 2.2: Genetic make-up and protocol). During these 3000 years burn-in, the model runs with temperature isocline speed T equaling 0 in the equation for $Y_{opt,t}$. After this burn-in we started our experiments.

Experiments

In the experiments the temperature isoclines were simulated to move northward for 600 years, under the different scenarios in Table 2.1. Each parameter setting was run twice in each landscape variant (10 runs in total). For studying trends in numbers of individuals and alleles, we averaged these per parameter setting. For individuals we averaged over the two runs of the five landscape variants, for alleles we also averaged over the 10 loci.

APPENDIX 2.2: GENETIC MAKE-UP AND PROTOCOL

The model species is diploid and its DNA consists of 10 unlinked loci (representing 1 locus at each of 10 different chromosomes). At initialisation of the model, each individual was randomly given 2 alleles per locus. All alleles are neutral and thus have no effect on individual performance. The mutation rate per generation in the model is 10^{-4} , equal to the estimated mutation rate for medium-sized microsatellites per haplotype per generation (Whittaker *et al.* 2003).

Since we wanted to monitor the level and distribution of genetic diversity under climate change, we first needed to establish equilibrium population genetics in the metapopulation. We regarded three aspects of population genetics: 1) the number of unique alleles, 2) the population structure, which is represented by the average differentiation among populations within the metapopulation, F_{ST} , and 3) the frequency distribution of the alleles.

1) In search for the number of alleles this metapopulation can contain under stable conditions, we tried various initialisations (see Initialisation and Burn-in in Appendix 2.1: Detailed model description). When we tried burn-ins of several hundreds generations initialised with 250, 100, and 50 unique alleles, randomly distributed among the initial individuals, we observed that the numbers of unique alleles steadily declined during these simulations. We then initialised with only 20 unique alleles and gave new alleles created through mutation a value between 21 and 50 in order to be able to observe them. In a simulated 1000 generations burn-in the equilibrium level of unique alleles was established after approximately 500 generations at approximately 33. When we tried to generate this equilibrium level of approximately 33 alleles by starting with a single allele, this took much longer, > 20 000 generations.

2) For a stable population structure we ran a burn-in of 20 000 generations and observed that the average F_{ST} value stabilised already after 2000 generations.

3) During burn-in runs, the allele frequency distribution tended towards a lognormal decline in allele frequencies from the most common to the least common allele (comparative to Ewens (1972) for the situation $\theta \gg 1$, where he observes a comparatively large number of low-frequency alleles). At most loci this distribution established after approximately 2000 generations. When we initialised with a single allele, this distribution establishment was not found within 20 000 generations of burn-in.

Based on these results we decided to initialise each model run with unique allele numbers ranging from 1 to 20. Mutations were given values between 21 and 50, to be able to distinguish between initial alleles and newly mutated alleles. We then allowed before each experiment a generous burn-in of 3000 generations, which established equilibrium F_{ST} values and allele frequency distributions.

APPENDIX 2.3: EXTRA FIGURES

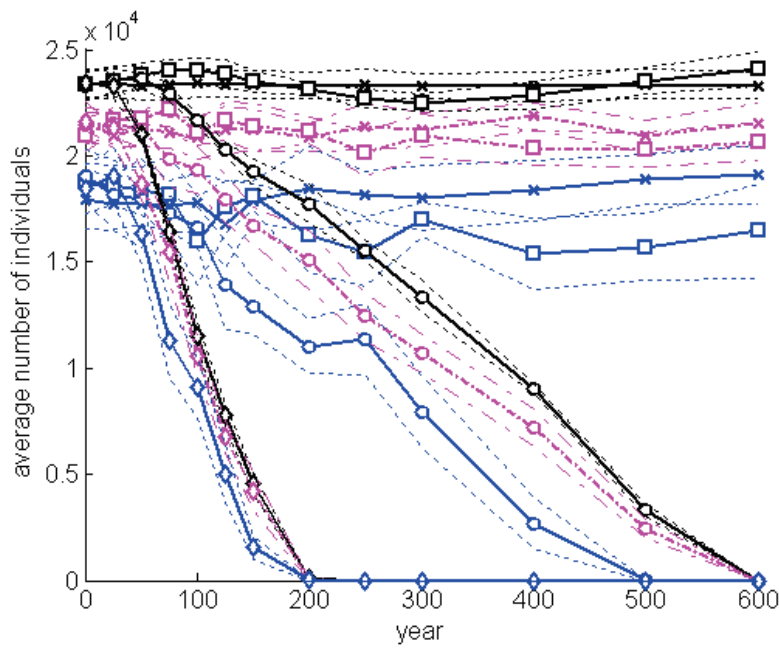


Figure 2.7a. Average number of individuals per year for all combined temperature isocline speeds 0 (-x-), 2 (-□-), 4 (-○-), and 8 (-◇-) km per year, and random weather variabilities of 0 (black), 140 (magenta) and 280 (blue) km. Dotted lines indicate confidence intervals.

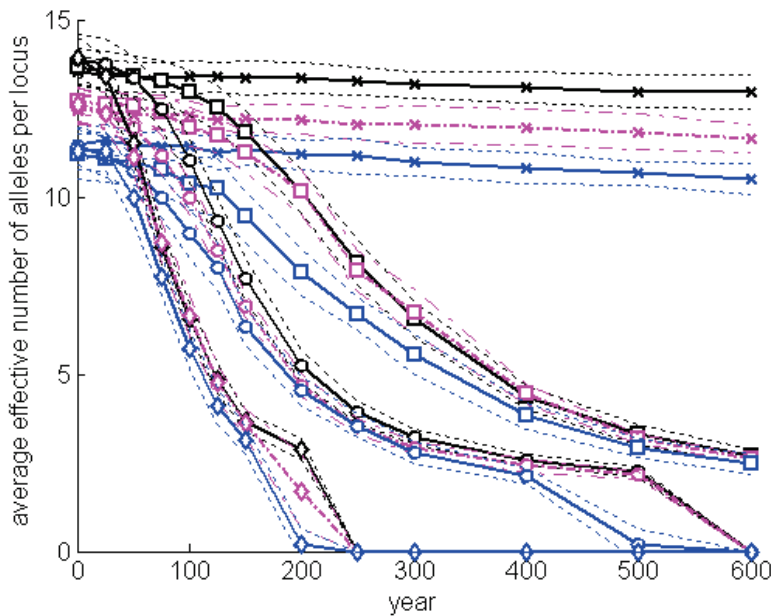


Figure 2.7b. Average effective number of alleles per locus per year for all combined temperature isocline speeds 0 (-x-), 2 (-□-), 4 (-○-), and 8 (-◇-) km per year, and random weather variabilities of 0 (black), 140 (magenta) and 280 (blue) km. Dotted lines indicate confidence intervals.

CHAPTER THREE

LANDSCAPE PREREQUISITES FOR THE SURVIVAL OF A MODELLED METAPOPOPULATION AND ITS GENETIC DIVERSITY ARE AFFECTED BY CLIMATE CHANGE

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ABSTRACT

In response to climate change a species may move, adapt, or go extinct. For the adaptability of a population its genetic diversity is essential, but climate change-induced range shifts can cause a loss of genetic diversity. We investigated how landscape structure affects the level and distribution of genetic diversity in metapopulations subject to climate change-induced range shifts. For this we used the spatially explicit, individual-based model METAPHOR which simulates metapopulation demography and genetics under different temperature increase scenarios. The results indicated that increasing total habitat area may enhance the maintenance of the genetic diversity in metapopulations while they are shifting their range under climate change. However, the results also showed that a high level of total habitat area did not prevent the populations in the newly colonised habitat area of being depleted of much of the original genetic diversity. We therefore conclude that enhancing landscape connectivity may lead to a delayed loss of genetic diversity in metapopulations under climate change, but that additional measures would be necessary to ensure its long-term conservation. Importantly, our simulations also show that a landscape which could be regarded as well-structured under stable climatic conditions, may be inferior for the conservation of genetic diversity during a range shift. This is important information for landscape management when developing strategies for the *in situ* conservation of genetic variation in natural populations under climate change.

INTRODUCTION

Climate change may invoke several responses from species. In response to current climate change species have been shown (see Parmesan 2006 for an overview) 1. to shift their ranges (e.g. Parmesan & Yohe 2003), 2. to rapidly evolve locally toward higher frequencies of beneficial genotypes under changed conditions, 3. to change their phenology (e.g. Visser & Both 2005), and 4. to go extinct, both locally and globally (e.g. Pounds *et al.* 2006). There is so far no evidence for evolution leading to a changed climate tolerance of species, but local adaptation may relieve the necessary magnitude of the range shift (Parmesan 2006).

Genetic variation is essential for the adaptability of a population. Hewitt (1996) has shown that range shifts in response to warming after the ice ages have led to local loss of genetic diversity for several species. This loss may be the result of the demographic process of range shift alone, so without losses resulting from selection, as has been shown in several modelling studies (Cobben *et al.* 2011, McInerney *et al.* 2009). Garroway *et al.* (2011) showed the same genetic signature in an empirical study of the range expansion of flying squirrel in response to contemporary climate change. We interpret these findings as a reason to develop a conservation strategy for maintaining genetic diversity in natural populations of species during range shift. However, there is no consensus on ways to monitor levels of genetic diversity, and discussion about this topic has only just begun (Laikre *et al.* 2008, Sgrò *et al.* 2011). Management strategies for conserving genetic diversity are currently mainly aimed at species in already well-managed systems, such as food production (Laikre *et al.* 2010), production or mixed-purpose forests (Koskela *et al.* 2007, Smulders *et al.* 2009), and captive breeding programs in zoos (Margan *et al.* 1998).

The genetic diversity has been *restored* in local populations of some protected species which were at the brink of extinction due to inbreeding depression (Madsen *et al.* 1999). Yet, such management strategies are not suitable for the structural conservation of genetic diversity in natural populations. Various landscape genetics studies have looked into the effects of landscape structure on the level of genetic diversity in populations of wild species (e.g. Arens *et al.* 2007, Balkenhol *et al.* 2009, Diekötter *et al.* 2010). Although such studies give valuable information on how landscape management could increase the conserved level of genetic variation (e.g. Vos *et al.* 2001a), they do not take into account the dynamics in populations caused by range shifts across the landscape as a response to temperature increase. Here we, for the first time, explore changes in genetic diversity in such geographical range shifts in different landscapes.

In fragmented landscapes species often survive as metapopulations (Hanski 1998). Metapopulation survival is dependent of the extinction probability of each population and its recolonisation rate. The combined extinction and recolonisation probabilities are determined by the cohesion of the habitat network, which is the result of the patch sizes and the dispersal stream across the landscape (Opdam *et al.* 2003). Four landscape components therefore affect the network cohesion: habitat quality, amount of habitat, spatial distribution of habitat and matrix permeability (Opdam *et al.* 2003). The amount of habitat and its distribution are the spatial components which we here define as the landscape structure. The genetic variation present in a species is the result of mutations, selection

and past and present demographic processes. These latter are in turn affected by the extinction and recolonisation processes in a metapopulation and are therefore dependent of the landscape structure as well.

Our purpose is to investigate how landscape structure affects the distribution of neutral genetic diversity in metapopulations subject to a range shift induced by the anticipated climate change. Additionally we assess how the sustainability of the habitat network for the metapopulation and its genetic diversity is affected by the predicted temperature increase. For this we use an individual-based, spatially explicit model as is suggested by Landguth *et al.* (2010) to study landscape genetics in complex landscapes. We vary three different landscape components: habitat amount, patch size and patch density, leading to landscape structures with habitat networks of different levels of patch extinction and recolonisation probabilities. Since we are interested in the demographic, and not the evolutionary effects, of landscape structure, we limit our scope to neutral genetic diversity. We believe our modelling approach is a further step towards the assessment of specific strategies for *in situ* conservation of high levels of genetic variation under climate change.

METHODS

For this study we used the same methodology as Cobben *et al.* (2011). We used METAPHOR, a simulation model for metapopulation demography (Verboom *et al.* 2001, Vos *et al.* 2001b) and genetics (Cobben *et al.* 2011) under stochastic temperature zone shifts (Schippers *et al.* 2011). All genes were selectively neutral. Reproduction, dispersal and survival were based on population density and habitat quality. Habitat quality was controlled by time and location specific temperature. As such we simulated the effect of stochastic temperature zone shifts on neutral genetic diversity. For detailed information see Appendix 3.1: Detailed model description and Appendix 3.2: Genetic make-up and protocol. Table 3.1 gives an overview of all species, gene and climate parameters used.

We modelled a woodland bird in several irregular landscapes. The model bird was parameterised as the middle spotted woodpecker (*Dendrocopus medius*), based on ecological information and on the interpretation by Schippers *et al.* (2011) (see Table 3.1 and Appendix 3.1: Detailed model description). Middle spotted woodpeckers are constricted to old oak forest. In The Netherlands, the total forest area makes up about 10% of the total land surface of the country. Oak forests, of all age categories, occupy about 2% of the Dutch land surface (Dirkse *et al.* 2007). We chose the landscapes to contain habitat amounts in the same order of magnitude. From their patch of origin individuals were allowed to disperse in every direction, along a straight line. Inter-patch connectivity was determined by destination patch radius and by distance from source to destination patch.

The temperature optimum shifted northwards across the landscape according to the temperature increase scenario used (see below and Table 3.1). Climate suitability was translated to a habitat patch quality ranging from 0 to 1. We used three temperature increase scenarios, based on work by the Hadley Centre (2003), of 1 °C, of 2 °C and of 4 °C temperature increase from year 2000 to 2100. The three scenarios were equivalent to isocline speeds of respectively 2, 4 and 8 km per year. The standard deviation of the current average temperature is 0.59 °C. This was translated to the standard deviation of

the location of the optimal temperature, corresponding to 140 km by Schippers *et al.* (2011). As such we modelled the increase and the variation in temperature as a spatial pattern of habitat qualities.

Table 3.1. The used model parameters. The species and climate parameters are those used by Cobben *et al.* (2011) and Schippers *et al.* (2011). The parameter names link this table to the functions in Appendix 3.1: Detailed model description.

Parameter description	Value	Unit	Parameter name
Species parameters			
<i>Recruitment</i>			
area per reproductive unit	5	ha	
recruitment at density = 0 and quality = 1	2.4	juveniles/female	N_{O_PD0HQ1}
recruitment at density = 1 and quality = 1	1.8	juveniles/female	N_{O_PD1HQ1}
recruitment at density = 0 and quality = 0	0	juveniles/female	N_{O_PD0HQ0}
<i>Dispersal</i>			
maximum dispersal distance	15	km	
maximum detection distance	150	m	l
juvenile dispersal probability:			
at density = 0 and quality = 1	0	year ⁻¹	P_{D_PD0HQ1}
at density = 1 and quality = 1	0.6	year ⁻¹	P_{D_PD1HQ1}
at density = 0 and quality = 0	1	year ⁻¹	P_{D_PD0HQ0}
adult dispersal probability:			
at density = 0 and quality = 1	0	year ⁻¹	P_{D_PD0HQ1}
at density = 1 and quality = 1	0.1	year ⁻¹	P_{D_PD1HQ1}
at density = 0 and quality = 0	0.5	year ⁻¹	P_{D_PD0HQ0}
<i>Survival</i>			
juvenile survival probability	1	year ⁻¹	P_{S_PD0HQ1} , P_{S_PD1HQ1} , P_{S_PD0HQ0}
adult survival probability at quality = 1	0.8	year ⁻¹	P_{S_PD0HQ1} , P_{S_PD1HQ1} , P_{S_PD0HQ0}
adult survival probability at quality = 0	0.55	year ⁻¹	P_{S_PD0HQ1} , P_{S_PD1HQ1} , P_{S_PD0HQ0}
Genetic parameters			
allele range at initialisation	1-20		
allele range after mutation	21-50		
mutation rate	10 ⁻⁴	generation ⁻¹	
Climate parameters			
temperature isocline speed	2, 4, 8	km year ⁻¹	T
weather variability	140	km	σ_d
temperature tolerance	800	km	H
initial temperature optimum location	400	km from the south edge	$Y_{opt,0}$
Model run parameters			
burn-in	3000	years	
investigated time points after burn-in	0, 25, 50, 75, 100, 125, 150, 200, 250, 300, 400, 500, 600	years	

At initialisation of the model, all habitat patches were filled with 10 adult individuals, equaling half the carrying capacity. Each individual was randomly given 2 alleles per locus for 10 different, unlinked loci. We allowed for mutations at a rate of 10^{-4} per generation (e.g. Whittaker *et al.* 2003). To obtain the equilibrium situation we allowed a generous burn-in of 3000 generations after initialisation.

Simulation experiments

We designed a base landscape, consisting of 3000 randomly positioned patches of 50 ha, so containing a total of 5% habitat area (see Figure 3.1, landscape C). We created two landscape types with 2.5% habitat area, both by halving the patch size (landscape B), and by halving the number of patches (landscape A). We furthermore created two landscape types with 10% habitat area, both by doubling the patch size (landscape D), and by doubling the number of patches (landscape E). See Table 3.2 for the characteristics of the landscape types. So along landscapes A-C-E there is an increase in patch density, with reduced inter-patch distances but with equal patch sizes. Landscape series B-C-D show the same increase in total habitat area through an increase in patch size, with similar inter-patch distances. The combinations of landscapes A-B and D-E give the opportunity to compare model outcomes between different spatial configurations with the same total habitat area.

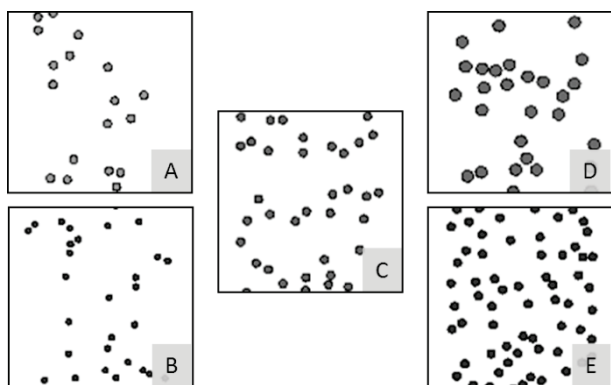


Figure 3.1. Examples of the five landscape types used. The landscape series A-C-E shows an increase in habitat amount by increasing the number of patches. The landscape series B-C-D shows an increase in habitat amount by increasing the size of the patches. The pictures show the kilometers 208-225 of the first of the five realisations of each of the landscape types.

Table 3.2. The features of the used landscape types.

<i>total habitat area</i>		
2.5%	5%	10%
A. 1500 patches of 50 ha	C. 3000 patches of 50 ha	D. 3000 patches of 100 ha
B. 3000 patches of 25 ha		E. 6000 patches of 50 ha

In experiment 1 we compared the distributions of neutral genetic diversity between the different landscapes under the temperature increase scenarios. For determining the network cohesion of the landscapes under climate change we assessed the metapopulation size and the level of neutral genetic diversity in each landscape in time during the temperature increase scenarios in experiment 2.

In the experiments the temperature isoclines were simulated to move northward across the landscapes for 600 years according to the three climate scenario speeds and one control speed of zero km per year. For each of the five investigated landscapes we randomly generated five variants. Each simulated parameter setting was repeated twice in each landscape variant.

Analysis

We investigated how level and distribution of neutral genetic diversity changed while the species shifted its range by moving through the model landscape. This diversity was expressed by two measures of genetic diversity: the average actual number of alleles per locus (A) and the average effective number of alleles per locus (A_e), following the equation (Frankham *et al.* 2005):

$$A_e = \frac{1}{\sum_i p_i^2},$$

where p_i denotes the frequency of allele i in the population. Differences between A and A_e provide information about low-frequency alleles, including new mutations. Both for the whole metapopulation and per zone of 50 km, we analysed the changes in these measures. For structuring the data and calculating the allele frequencies we used Genepop 4.0 (Rousset 2008). For studying trends in numbers of individuals and alleles, these were averaged per parameter setting. For individuals we averaged over the two runs of the five landscape variants, for alleles additionally over the 10 loci. Confidence intervals showed variation between different runs.

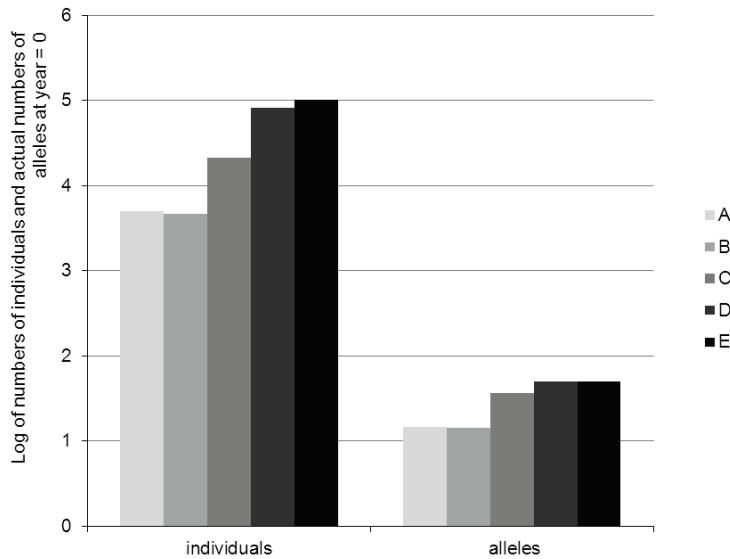


Figure 3.2. The initial (year = 0) number of individuals and the initial actual number of neutral alleles in the five landscape structures

RESULTS

The effects of landscape structure on the distribution of neutral genetic diversity

The landscape structure had a pronounced effect on the initial metapopulation size and its level of neutral genetic diversity (see Figure 3.2). Landscape E, with 10% habitat area and patch size of 50 ha, contained most individuals and alleles, while landscape B, with 2.5% habitat area and patch sizes of 25 ha, could house the smallest number of individuals and alleles. Under temperature increase the alleles showed a skewed geographical distribution in all landscapes (see Figure 3.3). The landscape structure did affect the timing of reaching a certain level of skew of the allele distribution. Here we compared the

landscapes with the initially largest metapopulation (E) and the smallest metapopulation (B). The Figures 3.3a and 3.3b show a similar level of skew of the allele distribution in the respective landscapes B and E. In the newly colonised area under temperature increase, so north of the indicator line, the average actual number of alleles per range ($mean_A$) was 58% of the $mean_A$ in the original territory south of the line in landscape B (Figure 3.3a) after 250 years of temperature increase. In landscape E (Figure 3.3b) this was a similar level of 64% after 500 years of temperature increase.

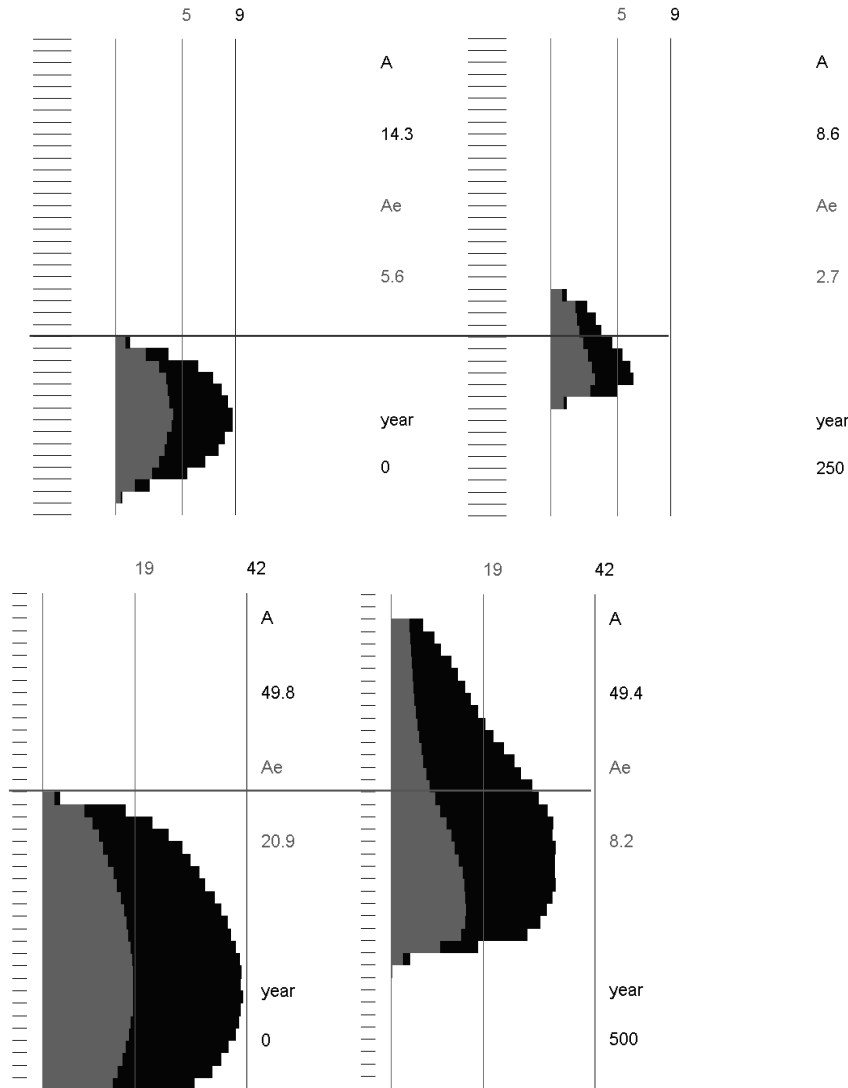


Figure 3.3. The spatial distribution of the numbers of neutral alleles (black) and the effective numbers of neutral alleles (grey) in the landscapes B (a) and E (b) after a period of temperature optimum move of 2 km year⁻¹. The distributions show a similar skew but after a period of respectively 250 and 500 years. The populations were grouped in 50 km ranges, displayed as the horizontal lines. The dark grey horizontal lines across the two figures in both a) and b) indicate the borders between the old range and the area colonised after the start of the temperature increase. A and A_e indicate respectively the total number of alleles and the effective number of alleles for the whole metapopulation in the given year. The vertical lines serve as scales and indicate the found maximum actual and effective numbers of alleles in any 50 km range across all investigated time points. Weather variability was 140 km.

The effects of temperature increase on the sustainability of the habitat network for the metapopulation and its neutral genetic diversity

The shifting metapopulation ranges under temperature increase led to loss of neutral genetic diversity in all landscapes. The rate of loss of neutral genetic diversity depended on the landscape structure and on the rate of temperature increase. The half-life of the initial number of alleles in the metapopulation was larger when the temperature increase was smaller (Figure 3.4). Landscapes A and B performed worst in maintaining their levels of genetic diversity, while landscape D showed the largest half-life of its initial numbers of alleles (Figure 3.4). This is in contrast with landscape E having the largest initial numbers of individuals and alleles as we showed in the previous Results section. Regarding the numbers of individuals in the landscapes we therefore focus here on the difference between landscapes D and E. Under the temperature increase scenario of 2 km/year the metapopulations in these landscapes were not declining and the difference between the sizes in the two landscapes was constant in time (Figure 3.5a). With the 4 km/year shift of the temperature isoclines individual numbers were decreasing in time with a larger rate of decline in landscape E (Figure 3.5b). Under the temperature isocline move of 8 km/year we observed that the rate of decline of the metapopulation size was larger for landscape E than for D (Figure 3.5c), to the extent that at a certain point the metapopulation size in landscape D was larger than in landscape E.

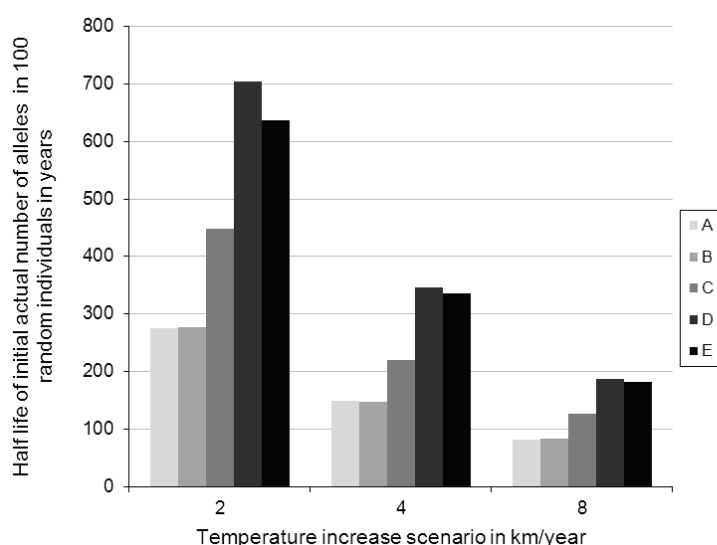


Figure 3.4. The half-life in years of the average actual number of neutral alleles in samples of 100 random individuals for the five landscape structures and the three temperature increase scenarios.

DISCUSSION

The purpose of this study was to investigate 1) how landscape structure may affect the distribution of neutral genetic diversity in a species range under range shifts induced by the predicted climate change, and 2) how the habitat network cohesion, determining the persistence of the metapopulation and its genetic diversity, was affected by the temperature increase. For this we modelled both the demography and the genetics of a species with medium dispersal capacity in a metapopulation setting under climate-

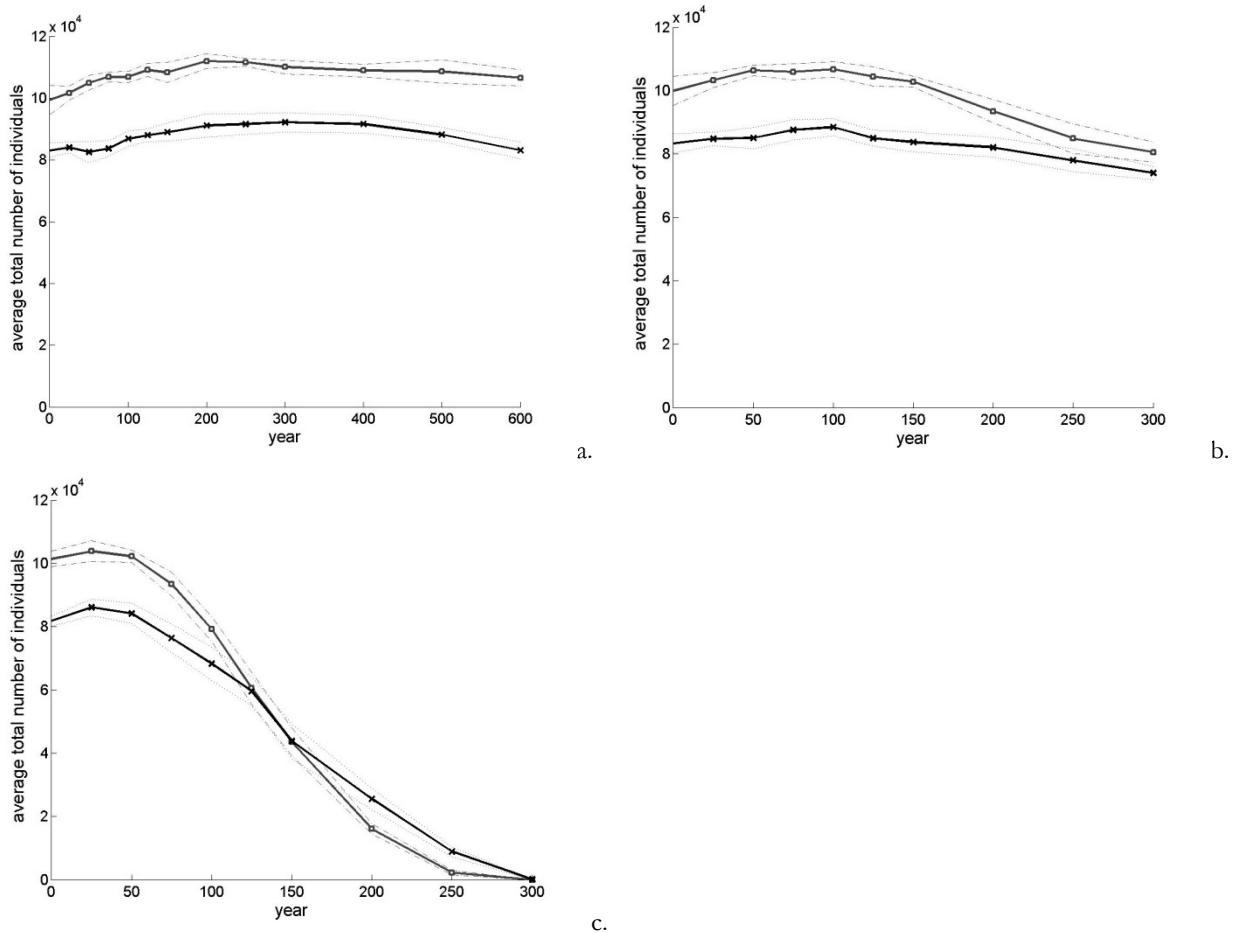


Figure 3.5. The metapopulation size N in time in the landscapes D (3000 patches of 100 ha, -x-) and E (6000 patches of 50 ha, -□-) with their 95% confidence intervals under temperature increase scenarios of 2 km/year (a), 4 km/year (b) and 8 km/year (c).

induced range shifts in landscapes with different levels of total habitat area, patch size and patch density.

The landscape structure had a pronounced effect on the initial metapopulation size and the level of genetic diversity with a clear dominance of the total habitat area component. However, the changes in landscape components among the investigated landscapes would not prevent a skew in the spatial distribution of the genetic diversity in time under temperature increase. The timing and level of the skew was affected by the landscape structure, showing a delay of skew in landscapes with larger total habitat areas.

Landscapes with large total habitat area could contain the largest metapopulations and levels of neutral genetic diversity. The sustainability of a specific landscape structure for the metapopulation was affected by the level of temperature increase. These results suggest that network cohesion is the result of the interaction of landscape structure, species characteristics and environmental dynamics.

Initial metapopulation sizes in the different landscapes

The total habitat area in the landscape showed a clear positive effect on the initial metapopulation size and its level of genetic diversity. The effects of patch size and patch density were less obvious. Under small total habitat area the metapopulation size was more constrained by the smaller patch size, while

under the large habitat amount its size was limited by the larger inter-patch distances. This result suggests that it is important to always take into account species-specific responses to landscape structure, as was stated by Taylor *et al* (2006).

Skew in spatial distribution of genetic diversity under temperature increase

Cobben *et al.* (2011) showed that neutral genetic diversity in metapopulations under climate change induced range shifts takes a skewed distribution in time, as was found for many species after the last ice age (Hewitt 1996) and for flying squirrel under contemporary climate change (Garroway *et al.* 2011). In this study in time, the spatial distribution of the neutral genetic diversity would become skewed as well under temperature increase in all landscapes. This skew was caused by repeated founder effects, leading to colonisation of the newly available habitat patches by a small subset of alleles, while the other alleles would remain in the original metapopulation range. This process could not be prevented in any of the investigated landscapes. However, the landscape structure did affect the timing and level of the skew which was the result of differences in the initial metapopulation range between the different landscapes. In landscapes with more habitat area the metapopulation took longer to disperse out of its original range, because this range was larger. This delayed the change in neutral allele distribution compared to landscapes with a smaller total habitat area.

Changing network cohesion under different levels of climate change

Landscape D, with 3000 patches of 100 ha performed the best in maintaining the metapopulation size and its neutral genetic diversity under temperature increase. This is in contrast with landscape E, with 6000 patches of 50 ha, housing the largest metapopulation and level of neutral genetic diversity under stable conditions. Landscape D had the largest patch sizes, so the smallest population extinction rate, but as a result of the lower number of patches, the inter-patch distances were on average larger than in landscape E. Under stable climate conditions, only including the current weather variability, the species profited from the smaller distances between patches in landscape E. Throughout the range it was easier to find a new patch because of the smaller distances and the higher availability of habitat patches. This decreased the dispersal mortality and led to larger overall habitat occupation in landscape E compared to D. Under temperature increase the situation changed. The range expansion at the leading edge of the metapopulation was not limited by the distances between patches but by the rate with which populations were established and capable of producing new dispersers. The larger habitat patches and smaller number of patches in landscape D compared to landscape E increased the rate of population establishment and thus of the range expansion. At the lagging edge of the metapopulation the populations could persist for a longer time in landscape D when habitat quality was decreasing. This was the result of the larger patch sizes leading to larger populations which could withstand the increasing frequency of bad years for a longer time period compared to the populations in landscape E. Since these southern populations carried most of the genetic diversity after a period of temperature increase (Cobben *et al.* 2011) the half-life of the initial number of alleles in the metapopulation in landscape D would therefore also be larger.

Perspectives

In our study the different landscapes remained unchanged from the burn-in phase of the simulation runs into the temperature increase phase. In reality, landscapes are not stable, and the genetic diversity we measure in the field today is the result of the combination of historical and current processes in differently shaped landscapes (Arens *et al.* 2007, Balkenhol *et al.* 2009, Vos *et al.* 2001a). To assess the effects of landscape structure in our model it would have been more accurate to run the burn-in in a 'historic', unaffected landscape and change the landscape structure after this burn-in phase by first decreasing patches sizes and total habitat area as a result of habitat destruction and fragmentation, and subsequently increasing them again to assess their value as a conservation strategy. However, these changes would lead to large transition effects in the metapopulation size and the level of neutral genetic diversity, and as such blur the genuine effects of landscape structure and range shift. Such transitions are however currently occurring in our natural areas (as becomes clear from studies such as e.g. Arens *et al.* 2007, Metzger *et al.* 2009). More research is needed to pinpoint them and to find out how to deal with them in biodiversity conservation management (Zellmer & Knowles 2009).

We investigated the effects of landscape structure on the level and distribution of neutral genetic diversity. In general the level of neutral genetic diversity may be considered a poor proxy for the level of adaptive genetic diversity in a population (Holderegger *et al.* 2006). However, when studying the landscape structure the use of adaptive genetic diversity is inappropriate since changes therein will reflect both demographic and evolutionary changes (Excoffier *et al.* 2009). Ficetola & Bonin (2011) elaborate on how information from both neutral and adaptive markers may supplement each other (Richter-Boix *et al.* 2011) to assess the influence of landscape features on the conservation of adaptive genetic diversity. More research is required to model such processes to be able to make valid predictions about the conservation of adaptive genetic diversity under climate change.

Here we investigated the effects of landscape structure on the survival of a metapopulation of the middle spotted woodpecker and its neutral genetic diversity. However, network cohesion is affected by other factors, such as e.g. habitat quality and heterogeneity, the permeability of the landscape matrix, the specific species and its life history traits (Opdam *et al.* 2003). Although our study gives a general insight into what effects may and may not be expected from changes in total habitat area, patch size and patch density regarding the conservation of neutral genetic diversity, this definition makes clear that the assessment of specific strategies for *in situ* conserving of high levels of genetic variation should be investigated location and species specifically.

The total habitat areas in this study were varied from 2.5% to 10% of the total landscape area. This range was chosen to comply with actual percentages of forest in general and oak forest in particular in The Netherlands. However, internationally these percentages may be considered relatively low. Our study showed a clear effect of increased total habitat area on the metapopulation size and its level of genetic diversity both under stable and changing climate conditions, and on the timing and level of the skew in genetic diversity under temperature increase. We believe that the strength of this effect gives a good indication that further increase of total habitat area in the landscape has increased

beneficial consequences. However, we feel that the chosen range of level of total habitat area is fairly representative for species suffering from habitat fragmentation.

Implications for landscape management

The effect of landscape structure on population demography under climate change has been investigated by e.g. Vos *et al.* (2008). They found that increasing landscape connectivity may be a sufficient measure to facilitate range shifts leading to species conservation under climate change. Cobben *et al.* (2011) found that range shifts induced by the predicted temperature increase lead to loss of neutral genetic diversity in the metapopulation, even if the metapopulation size remains unaffected. The results of this study indicate that landscape structure may enhance the survival of the present neutral genetic diversity in metapopulations which are shifting their ranges under climate change. However, repeated founder effects under metapopulation range shifts and the eventual genetic depletion in the populations in the newly colonised habitat area could not be prevented. We therefore conclude that increasing total habitat area may lead to a delayed extinction of genetic diversity in natural metapopulations under climate change, but additional measures would be necessary to ensure its long-term conservation. Such a measure could be the *ex situ* conservation of genetic material through a gene bank. This is more common for plants, although zoos currently provide such a service for many threatened species (Margan *et al.* 1998). Another measure, to conserve present genes *in situ* could consist of, regularly, transferring individuals with different genotypes to the expanding range margin to increase the chance of their spreading into the newly colonised region (Smulders *et al.* 2009). Both measures raise questions about ethics, logistics and finances and the latter management strategy would require much more research into its ecological feasibility. Our second conclusion is that a landscape structure with a large network cohesion under stable conditions may be inferior for the conservation of genetic diversity when range shifts are taken into account. This is important information for landscape management when developing strategies for the *in situ* conservation of genetic variation in natural populations under climate change.

APPENDIX 3.1: DETAILED MODEL DESCRIPTION

For this study we used the same methodology as Cobben *et al.* (2011). We used METAPHOR, a simulation model for metapopulation demography (Verboom *et al.* 2001, Vos *et al.* 2001b) and genetics (Cobben *et al.* 2011) under stochastic temperature zone shifts (Schippers *et al.* 2011). Population genetics in our model was the result of population demography. There was no reciprocal effect of genetics on demography, since all genes were assumed to be selectively neutral. The yearly metapopulation demography is simulated based on four events: reproduction, dispersal, survival and aging, in this order. Reproduction, dispersal and survival were based on population density and habitat quality. Habitat quality was controlled by time and location specific temperature. As such we simulated the effect of stochastic temperature zone shifts on neutral genetic diversity.

Landscape

Our model landscape had dimensions of 15 km from east to west by 2000 km from north to south. The east and west side were merged to create a cylindric landscape which diminished edge effects. The base landscape type contained 3000 patches of 50 ha each. To assess the effects of habitat amount and habitat fragmentation we generated four more landscape types in which we varied the numbers and sizes of the patches (see section Simulation Experiments). Within a landscape type however, all patches were of equal size. Patches were placed in random positions in the landscape, but were excluded from a buffer area within 150 m from existing patches. For each of the five investigated landscape types we randomly generated five variants.

Species

We modelled a woodland bird, parameterised as the middle spotted woodpecker (*Dendrocopus medius*). Parameters were based on biological information (Hagemeijer & Blair 1997, Kosenko & Kaigorodova 2001, Kosinski *et al.* 2004, Kosinski & Ksit 2006, Michalek & Winkler 2001, Pasinelli 2000, Pettersson 1985a, Pettersson 1985b) and on the interpretation by Schippers *et al.* (2011) (see Table 3.1). The model distinguishes 2 sexes and 2 lifestages: adults and juveniles. The yearly life cycle consists of recruitment, dispersal, and survival, in this order. Lastly, all juveniles age to adults. Recruitment, dispersal and survival are all dependent of life stage, population density (PD) and habitat quality (HQ).

$$PD = N_i / CC,$$

with N_i : number of individuals in patch,

CC : carrying capacity of patch, and

HQ : see section Climate in this appendix.

Species: recruitment function

The number of nests in a patch in each generation is equal to the number of unique adult pairs of opposite sex in this patch, with a maximum of 10. The number of offspring per nest is then found with:

$$N_O = N_{O_PD_0HQ_1} * \left(1 - \left(1 - \frac{N_{O_PD_0HQ_0}}{N_{O_PD_0HQ_1}} \right) * (1 - HQ) \right) * \left(1 - \left(1 - \frac{N_{O_PD_1HQ_1}}{N_{O_PD_0HQ_1}} \right) * PD \right)$$

with $N_{O_PD_0HQ_1}$: number of offspring at population density (PD) = 0 and habitat quality (HQ) = 1, and similar for $N_{O_PD_0HQ_0}$ and $N_{O_PD_1HQ_1}$. See Table 3.1.

Species: survival function

Determines for each individual the chance that it survives the current year, P_S .

$$P_S = P_{S_PD_0HQ_1} * \left(1 - \left(1 - \frac{P_{S_PD_0HQ_0}}{P_{S_PD_0HQ_1}} \right) * HQ \right) * \left(1 - \left(1 - \frac{P_{S_PD_1HQ_1}}{P_{S_PD_0HQ_1}} \right) * (1 - PD) \right)$$

with $P_{S_PD_0HQ_1}$: survival rate at population density (PD) = 0 and habitat quality (HQ) = 1, and similar for $P_{S_PD_0HQ_0}$ and $P_{S_PD_1HQ_1}$. See Table 3.1.

Species: dispersal function

Determines for each individual the yearly chance that it leaves its patch to go on dispersal, P_D .

$$P_D = P_{D_PD_0HQ_1} * \left(1 - \left(1 - \frac{P_{D_PD_0HQ_0}}{P_{D_PD_0HQ_1}} \right) * HQ \right) * \left(1 - \left(1 - \frac{P_{D_PD_1HQ_1}}{P_{D_PD_0HQ_1}} \right) * (1 - PD) \right)$$

with $P_{D_PD_1HQ_1}$: dispersal rate at population density (PD) = 1 and habitat quality (HQ) = 1, and similar for $P_{D_PD_1HQ_0}$ and $P_{D_PD_0HQ_1}$. See Table 3.1.

If an individual disperses, we need to determine where it goes. From their origin patch individuals can go in every direction, along a straight line. Connectivity to other patches is determined by destination patch radius (r) and distance to there (d). So the chance to disperse from patch A to patch B is:

$$P_{AB} = \frac{2 * \arcsin\left(\frac{r_B + l}{d_{AB}}\right)}{2\pi}$$

with l is 150 m, the maximum distance from where an individual can detect suitable habitat. The maximum dispersal distance is 15 km, so habitat patches that are separated by more than this distance

are not connected at all. Our model does not allow dispersers to ignore a nearer patch, so more distant patches are located in the shadow of the nearer patch. An individual may arrive in a patch with a population size larger than carrying capacity twice per dispersal event, and is then allowed to disperse again. Should it fail to reach a habitable patch within a total of three dispersal rounds, it dies.

Climate

Climate is incorporated in the model through habitat quality. Where climate is optimal for the species, habitat quality equals 1, and where climate is unsuitable for the species, habitat quality is 0 (see equation HQ below). Climate change scenarios are based on temperature increase predictions (I °C year⁻¹) by the Hadley Centre (2003) of 0.0167 and 0.0333 °C year⁻¹, and we also included a scenario with a temperature increase of 0.084 °C year⁻¹. Besides, the used scenarios include weather variability increase assumptions as temporal stochasticity in the temperature (the current standard deviation of the average temperature σ_t (°C), 0.59 °C (Schippers *et al.* 2011). Climate in our model is thus defined as the temperature in year t and at location Y . Climate change is then the speed with which temperature isoclines travel north (T km year⁻¹) and the yearly fluctuation of these lines (σ_d km). We use a climatic gradient from south to north of G (°C km⁻¹) to get to:

$$T = I / G, \text{ and}$$

$$\sigma_d = \sigma_t / G$$

This results in a current yearly fluctuation of the temperature isoclines σ_d of 140 km, and we further included scenarios with yearly fluctuations σ_d of 0 km and 280 km. We can then calculate the location of the optimal temperature in north-south direction (Y_{opt}) in a certain year as:

$$Y_{opt,t} = Y_{opt,0} + T * t + \sigma_d * N_t$$

with N_t is the yearly random number drawn from a standard normal distribution.

We obtain a normal habitat quality distribution with this optimal coordinate Y_{opt} in its centre by defining habitat quality (HQ) as

$$HQ_{patch,t} = \exp\left[\frac{-0.695(Y_{opt,t} - Y_{patch})^2}{H^2}\right]$$

H is an indicator of the temperature tolerance of the species, and defined as the distance from the temperature optimum at which habitat quality is 0.5. See Table 3.1.

Initialisation

At initialisation of the model, all habitat patches were filled with 10 adult individuals, equaling half the carrying capacity. Each individual was randomly given 2 alleles per locus for 10 different, unlinked loci

(for more detailed information see Appendix 3.2: Genetic make-up and protocol). The climate optimum Y_{opt} was initialised at 400 km from the southern landscape edge.

Burn-in

After initialisation the model was run for 3000 generations, thus 3000 years (for more detailed information see Appendix 3.2: Genetic make-up and protocol). During these 3000 years burn-in, the model runs with temperature isocline speed T equaling 0 in the equation for $Y_{opt,t}$. After this burn-in we started our experiments.

Experiments

In the experiments the temperature isoclines were simulated to move northward for 600 years, under the different scenarios in Table 3.1. Each parameter setting was run twice in each landscape variant (10 runs in total). For studying trends in numbers of individuals and alleles, we averaged these per parameter setting. For individuals we averaged over the two runs of the five landscape variants, for alleles also over the 10 loci.

APPENDIX 3.2: GENETIC MAKE-UP AND PROTOCOL

The model species has a diploid genome of 10 unlinked genes (representing 1 locus at each of 10 different chromosomes). At initialisation of the model, each individual was randomly given 2 alleles per locus. All alleles are neutral and thus have no effect on individual performance. The mutation rate per generation in the model is 10^{-4} , equal to the estimated mutation rate for medium-sized microsatellites per haplotype per generation (Whittaker *et al.* 2003).

Since we wanted to monitor the level and distribution of genetic diversity under climate change, we first needed to establish equilibrium population genetics in the metapopulation. We regarded three aspects of population genetics: 1) the number of unique alleles, 2) the population structure, which is represented by the average differentiation among populations within the metapopulation, F_{ST} , and 3) the frequency distribution of the alleles.

1) In search for the number of alleles this metapopulation can contain under stable conditions, we tried various initialisations (see Initialisation and Burn-in in Appendix 3.1: Detailed model description). When we tried burn-ins of several hundreds of generations initialised with 250, 100, and 50 unique alleles, randomly distributed among the initial individuals, we observed that the numbers of unique alleles steadily declined during these simulations. We then initialised with only 20 unique alleles and gave new alleles created through mutation a value between 21 and 50 in order to be able to observe them. In a simulated 1000 generations burn-in the equilibrium level of unique alleles was established after approximately 500 generations at approximately 33. When we tried to generate this equilibrium level of approximately 33 alleles by starting with a single allele, this took much longer, > 20 000 generations.

2) For a stable population structure we ran a burn-in of 20 000 generations and observed that the average F_{ST} value stabilised already after 2000 generations.

3) During burn-in runs, the allele frequency distribution tended towards a lognormal decline in allele frequencies from the most common to the least common allele (comparative to Ewens (1972) for the situation $\theta \gg 1$, where he observes a comparatively large number of low-frequency alleles). At most loci this distribution established after approximately 2000 generations. When we initialised with a single allele, this distribution establishment was not found within 20 000 generations of burn-in.

Based on these results we decided to initialise each model run with unique allele numbers ranging from 1 to 20. Mutations were given values between 21 and 50, to be able to distinguish between initial alleles and newly mutated alleles. We then allowed before each experiment a generous burn-in of 3000 generations, which established equilibrium F_{ST} values and allele frequency distributions.

CHAPTER FOUR

WRONG PLACE, WRONG TIME: CLIMATE CHANGE-INDUCED RANGE SHIFT ACROSS FRAGMENTED HABITAT CAUSES MALADAPTATION AND DECLINED POPULATION SIZE IN A MODELLED BIRD SPECIES

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ABSTRACT

Many species are locally adapted to decreased habitat quality at their range margins, and therefore show genetic differences along their ranges. The range shifts induced by contemporary climate change may affect local evolutionary processes at the expanding range margin due to founder events. Besides, the populations that are newly formed at the expanding range margin will in the course of time become located in the centre of the species' range. Recent studies investigated evolutionary changes at the expanding range margin, without assessing eventual effects across the species' range. We explored the possible influence of range shift on the level of adaptation throughout a species' range. For this we used a spatially explicit, individual-based simulation model of a woodland bird, parameterised after the middle spotted woodpecker (*Dendrocopus medius*) in fragmented habitat. We simulated its range under climate change, and incorporated genetic differences at a single locus that determined the individual's degree of adaptation to optimal temperature conditions. Generalist individuals had a large thermal tolerance but relatively low overall fitness, while climate specialists had a high fitness combined with a small thermal tolerance. In equilibrium the specialists inhabited the populations in the centre of the range, while the generalists dominated the margins. Under temperature increase, the generalist numbers increased at the expanding margin and eventually also occupied the centre of the shifting range, while the specialists ended up in the retracting margin. This was caused by founder events and led to overall maladaptation of the species, resulting in a declined metapopulation size and thus impeded species' persistence. Thus, we found no evidence for a complementary effect of local adaptation and range shifts on species' survival. Instead we showed that founder events can cause local maladaptation which can amplify throughout the species' range, and as such hamper the species' persistence under climate change.

INTRODUCTION

The genetic variation in a population of a natural species is the result of the interaction of adaptation to environmental conditions and population demography. Because conditions across a species' biogeographical range vary, many species show genetic differences between central and marginal populations (Sexton *et al.* 2009). Populations in species' range margins have shown adaptation to the average lower habitat quality (Kawecki 2008).

Under contemporary climate change (IPCC 2007) many species have been observed to shift their ranges corresponding to the increased temperature (Chen *et al.* 2011, Parmesan & Yohe 2003, Root *et al.* 2003). Range shifts may have genetic consequences such as founder events occurring at the expanding margins of such ranges (Garroway *et al.* 2011, Hill *et al.* 2011, Lee 2002, Mayr 1942). These can affect local evolutionary processes (Excoffier *et al.* 2009, Travis *et al.* 2007, Vila *et al.* 2003) and have been observed to generate signatures of declined neutral genetic variation in recently established populations (Excoffier *et al.* 2009, Hewitt 1996, Hill *et al.* 2011). Contemporary climate change may thus affect the frequencies of genotypes in populations at species' range margins. Furthermore, under range shift the locations of these populations, originally at the range margin, will shift closer to the species' range centre, while the populations at the retracting range margin go extinct. Combined with the observed persistence of the founder effect (Hewitt 1996), this may eventually influence the genotype frequencies across the entire species' range (Cobben *et al.* 2011, Hewitt 1996, McInerny *et al.* 2009), and therefore the overall degree of adaptation to local conditions. Because this may result in local maladaptation and, consequently, decreased population sizes and persistence, it is of importance to understand how species' responses to climate change interact with the heterogeneous genetic structure throughout their ranges.

Changes in local adaptive genetic diversity under climate change have mainly been investigated in the expanding species' range margins and range interiors (Excoffier *et al.* 2009, Hill *et al.* 2011, Hill *et al.* 1999, Parmesan 2006, Thomas *et al.* 2001), with some research effort for the retracting range margins (Hampe & Petit 2005, Jump *et al.* 2006). Range-wide assessments exist mostly in modelling studies of neutral genetic diversity (Cobben *et al.* 2011, McInerny *et al.* 2009). Yet for past climate changes, founder events were shown to affect the genetic structure of populations in large parts of species' ranges (Hewitt 1996). Contemporary habitat fragmentation is furthermore likely to increase the occurrences and consequences of founder events upon range expansions, as can be deduced from theory (Mayr 1942) and simulations (Cobben *et al.* 2012, Edmonds *et al.* 2004, Klopstein *et al.* 2006). We therefore investigate the interaction of local adaptation and founder events across a species' range in fragmented habitat under climate change.

Here we simulate how a genetic difference in adaptation between central and marginal populations in a species' range along a temperature gradient in spatially structured habitat is affected by climate change, allowing for range shifts and local adaptation. For this we used a metapopulation based on ecological information of the middle spotted woodpecker (*Dendrocopos medius*), in which a single gene determines the degree of adaptation to local temperature conditions. Various climate change scenarios,

including both temperature increase and increased weather variability (Cobben *et al.* 2011, IPCC 2007, Schippers *et al.* 2011) were applied. We specifically asked:

- 1) how the local frequencies of the different genotypes in the species' range changed under range shifts,
- 2) how the changed distribution affected the persistence of the species, and
- 3) whether and when the original distribution of the various genotypes recovered after stabilisation of the temperature.

METHODS

For this study we used METAPHOR, a simulation model for metapopulation demography (Verboom *et al.* 2001, Vos *et al.* 2001b). The model has been extended to allow for stochastic temperature increase by Schippers *et al.* (2011). Here we further extended the model with a genetic module for adaptive traits. Reproduction, dispersal and survival were based on population density and habitat quality. The perceived habitat quality was controlled by the individual's genotype and the time and location specific temperature. As such we could simulate the effect of stochastic temperature increase on the spatial distribution of the different genotypes. For detailed information see Appendix 4.1. Table 4.1 gives an overview of all species, gene and climate parameters used.

The landscape we used in the model represented a north to south section through a virtual species range, which we used to follow the spatial shift of the species as a result of local population dynamics. It had dimensions of 15 km from east to west by 2000 km from north to south. The east and west side were merged to create a cylindric landscape, thus avoiding edge effects. The landscape contained 3000 circular habitat patches of 50 ha each (a total of 5% habitat) placed in random positions in the landscape, but at a minimum distance of 150 m from each other. Five landscape variants with different habitat positions were randomly generated and each simulated parameter setting was repeated twice in each landscape variant.

We modelled a woodland bird, parameterised as the middle spotted woodpecker *Dendrocopos medius* (Hagemeijer & Blair 1997, Kosenko & Kaigorodova 2001, Kosinski *et al.* 2004, Kosinski & Ksit 2006, Michalek & Winkler 2001, Pasinelli 2000, Pettersson 1985a, Pettersson 1985b) and interpretation by Schippers *et al.* (2011) (see Table 4.1). This species is a moderate disperser, yet not affected by infrastructural and urban barriers. It also is fairly specific in its habitat choice and has limited growth capacity. Therefore it represents a species of which the habitat distribution is fragmented over large areas, and with a population demography which makes it sensitive to range shifts. The model distinguished two sexes and two life stages. For this study we incorporated genetic differences among individuals of the species that determined their degree of adaptation to optimal temperature conditions. Recruitment, dispersal and survival were all dependent of population density and perceived habitat quality. From their origin patch individuals could disperse in every direction, along a straight line. Connectivity to other patches was determined by destination patch radius and by distance from original to destination patch. The maximum dispersal distance was 15 km, so habitat patches that were separated by more than this distance were not directly connected.

Table 4.1. Model parameters used. Names link this table to the functions in Appendix 4.1: Detailed model description.

Parameter description	Value	Unit	Parameter name
Landscape parameters			
number of patches	3000		
patch area	50	ha	
patch carrying capacity	20	individuals	
Species parameters			
perceived habitat quality genotype SS	1		$HQfactor_{gen}$
perceived habitat quality genotype SG	0.95		$HQfactor_{gen}$
perceived habitat quality genotype GG	0.9		$HQfactor_{gen}$
<i>Recruitment</i>			
area per reproductive unit	5	ha	
recruitment at density = 0 and quality = 1	2.4	juveniles/female	N_{O_PD0HQ1}
recruitment at density = 1 and quality = 1	1.8	juveniles/female	N_{O_PD1HQ1}
recruitment at density = 0 and quality = 0	0	juveniles/female	N_{O_PD0HQ0}
<i>Dispersal</i>			
maximum dispersal distance	15	km	
maximum detection distance	150	m	l
juvenile dispersal probability			
at density = 0 and quality = 1	0	year ⁻¹	P_{D_PD0HQ1}
at density = 1 and quality = 1	0.6	year ⁻¹	P_{D_PD1HQ1}
at density = 0 and quality = 0	1	year ⁻¹	P_{D_PD0HQ0}
adult dispersal probability			
at density = 0 and quality = 1	0	year ⁻¹	P_{D_PD0HQ1}
at density = 1 and quality = 1	0.1	year ⁻¹	P_{D_PD1HQ1}
at density = 0 and quality = 0	0.5	year ⁻¹	P_{D_PD1HQ0}
<i>Survival</i>			
juvenile survival probability	1	year ⁻¹	P_{S_PD0HQ1} , P_{S_PD1HQ1} , P_{S_PD0HQ0}
adult survival probability at quality = 1	0.8	year ⁻¹	P_{S_PD0HQ1} , P_{S_PD1HQ1} , P_{S_PD0HQ0}
adult survival probability at quality = 0	0.55	year ⁻¹	P_{S_PD0HQ1} , P_{S_PD1HQ1} , P_{S_PD0HQ0}
Genetic parameters			
allele range at initialisation	S and G		
allele range after mutation	S and G		
mutation rate	10 ⁻⁶	generation ⁻¹	
Climate parameters			
temperature isocline speed	2, 4, 8	km year ⁻¹	T
weather variability	0, 140, 280	km	σ_d
temperature tolerance genotype SS	600	km	H_{gen}
temperature tolerance genotype SG	700	km	H_{gen}
temperature tolerance genotype GG	800	km	H_{gen}
initial temperature optimum location	400	km from the south edge	$Y_{opt,0}$
Model run parameters			
burn-in	3000	years	
investigated time points after burn-in	0, 25, 50, 75, 100, 125, 150, 200, 250, 300, 400, 500, 600	years	

Under temperature increase the temperature optimum was shifting northwards across the species' range (see below and Table 4.1). Temperature suitability was translated to a habitat patch quality ranging from 0 to 1, based on distance from the climate optimum and on the half value parameter used, following a Gaussian curve (Schippers *et al.* 2011). We used three temperature increase scenarios, based on work by the Hadley Centre (2003). The first scenario was a temperature increase of 1 °C from year 2000 to 2100. For as far as we know now, this is an unrealistic prediction for the coming century but we incorporated it as an absolute minimal change to compare with the more likely scenarios of a 2 °C and 4 °C temperature increase by 2100 (HadleyCentre 2003). When translating these scenarios to temperature isocline shift rates we assumed that the simulated metapopulation was situated along the European Atlantic coast. Unaffected by mountain ranges it has a temperature gradient of 0.0042 °C per km (Schippers *et al.* 2011). The three scenarios were therefore equivalent to isocline shift rates of respectively 2, 4 and 8 km per year. The current standard deviation of the average temperature of 0.59 °C (Schippers *et al.* 2011) translated to a standard deviation of 140 km. To assess the effect of temperature variability we also applied levels of 280 km and 0 km.

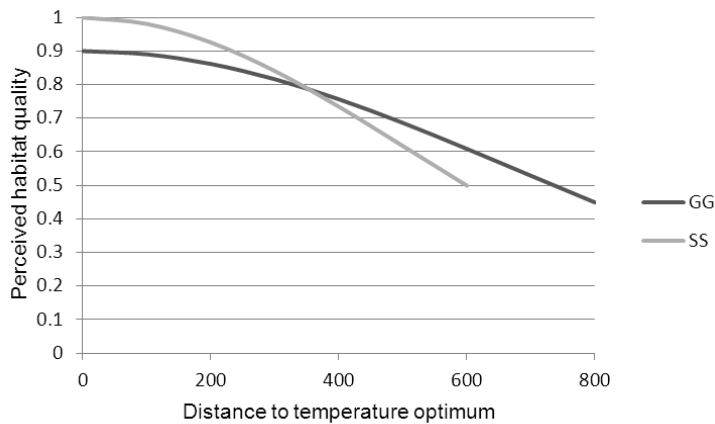


Figure 4.1. The perceived habitat quality, equivalent to relative fitness as a function of the individual's genotype and its distance to the temperature optimum. The GG-individuals are climate generalists, and the SS-individuals climate specialists.

We allowed two different alleles at the adaptive locus, the climate specialist allele S and the climate generalist allele G. Note that we use the terms specialist and generalist for the individuals carrying these different alleles, analogous to the use of these terms for different species, but we are dealing with different genotypes within one species. The alleles could mutate with frequency 10^{-6} (Nachman & Crowell 2000). Our species was diploid, leading to the three potential genotypes SS, SG and GG. The climate generalists, genotype GG, had a relatively large thermal tolerance but, as a trade-off, a lower overall fitness. The individuals' fitness was determined by local habitat quality, based on local and temporal temperature, as explained above. For the generalists we therefore restrained the perceived habitat quality, with a fitness factor of 0.9. The climate specialists with the SS genotype had a fitness factor of one, and thus no restrained habitat quality, but a relatively small thermal tolerance (see Figure 4.1). The individuals with the SG genotype were intermediate. Under equilibrium conditions this led to a distribution in which the specialists outcompeted the generalists at the range centre as a result of their higher fitness under optimal conditions, while the generalists outcompeted the specialists in the range margins as a result of their larger thermal tolerance. There were two transition areas at either side

of the temperature optimum where specialists, intermediates and generalists occurred together. The combination of the thermal tolerance and the distance to the climate optimum determined the local, genotype specific, habitat quality (Figure 4.1). The perceived habitat quality and the population density determined the survival rate, the number of offspring, and the dispersal rate. As such we created a metapopulation that, under equilibrium conditions, had an increasing dispersal rate and decreasing survival and recruitment rates from the centre to the range margin.

The model was initialised with 10 individuals in each habitat patch. These were randomly given 2 alleles. After initialisation we allowed a simulation of 3000 generations to obtain the equilibrium situation. During this burn-in phase, the model was run with no temperature zone shift but the simulated yearly temperature variability was already used. In the remainder of the paper, time 0 was set after the burn-in.

Simulation experiments

In this study we did three different model experiments.

1. To study how the local frequencies of the different genotypes in the species' range changed under climate change, we investigated the spatial distributions of the SS, SG and GG genotypes in time under nine climate change scenarios. Additionally we assessed the levels of neutral genetic diversity to check for the occurrence of founder events. For this we combined the three different rates of temperature isocline shift of 2 km/year, 4 km/year and 8 km/year with the three standard deviations 0 km, 140 km and 280 km. The temperature isoclines were simulated to move northward for 600 years.

2. To investigate how the changed genotype distributions affected the persistence of the species, we simulated the metapopulation, subjected to the three rates of temperature increase and the standard variation of 140 km, under two additional parameter settings. In these settings the metapopulation contained only one allele at the adaptation locus, so it had either only individuals of the SS genotype or of the GG genotype. We then assessed the size of the metapopulation under all three different parameter sets, so while containing only allele S, only allele G, or both alleles S and G, as was done in experiment 1.

3. To investigate the recovery of the original genotype distribution after stabilisation of the temperature, we subjected the metapopulation to the three temperature increase scenarios, which were stopped after 50 years or multiples of 50 years up to 700 years. The model was run for another 300 years after the stop with stabilised temperature, while documenting the genotype distributions.

Analysis

We stored and analysed data for several points in time (Table 4.1). To investigate the distribution of the genotypes we cut the landscape in ranges of 50 km and summed the numbers of individuals with the SS, SG, and GG genotypes in the combined populations in each 50 km range. For studying trends in numbers of individuals of the different genotypes, we averaged these per parameter setting over the two runs of the five landscape variants.

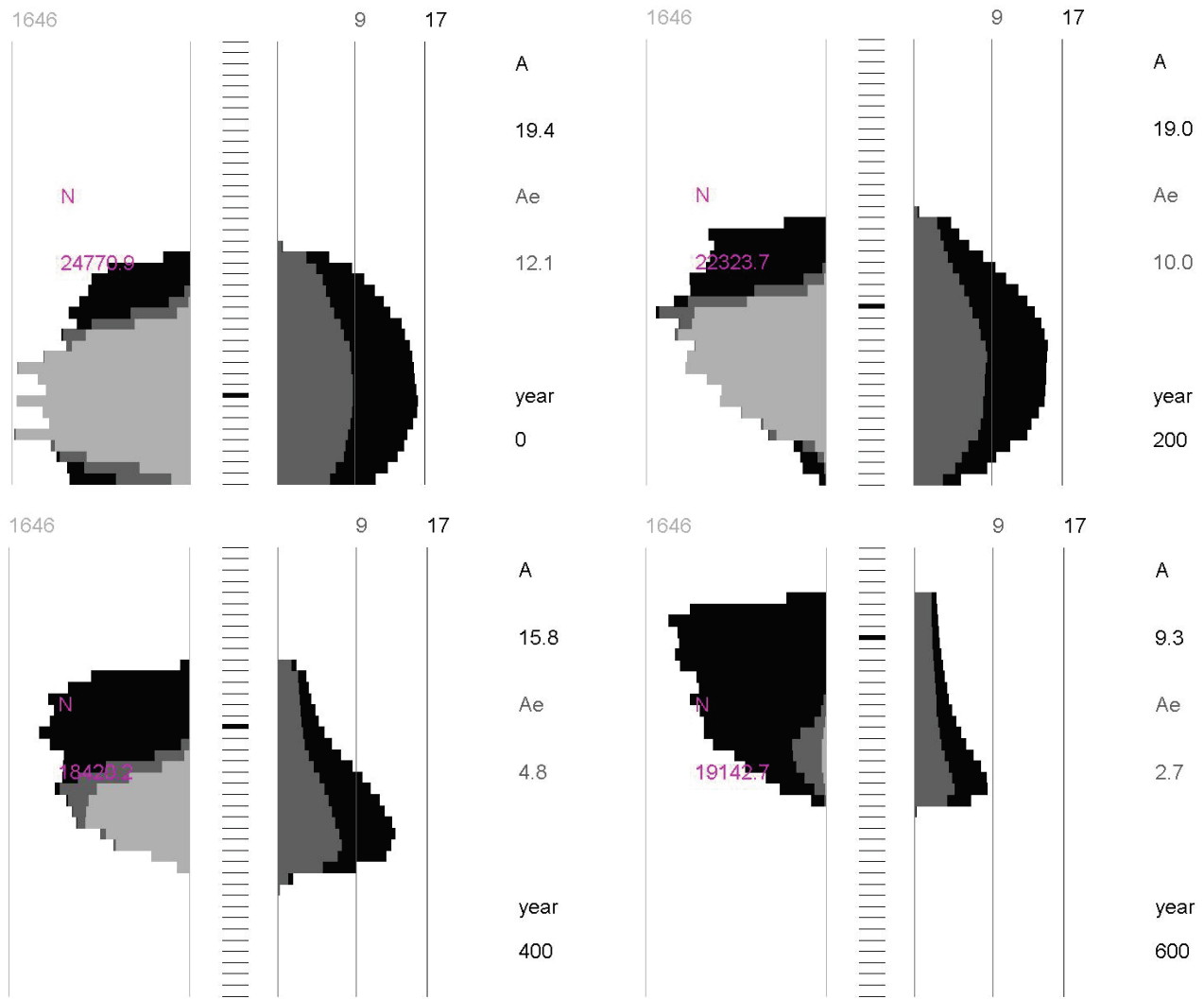


Figure 4.2. The distributions of the GG (left black), SG (left dark gray), and SS (left light gray) genotypes and the level of neutral genetic diversity in numbers (right black) and effective numbers (right dark gray) of alleles in time under the temperature isocline shift rate of 2 km/year, with standard deviation of 140 km. N, A and A_e respectively give the individual numbers, allele numbers and allele effective numbers in the total metapopulation. The bold black bars indicate the locations of the average temperature optimum along the total range of 2000 km. The vertical lines serve as scales and specifically note the maximum value in any of the range blocks of 50 km during the complete time series.

RESULTS

Effects of climate change on the spatial distribution of the genotypes

The original distribution of the genotypes in the metapopulation was changed under the range shift which was caused by the temperature increase (Figure 4.2). This led to an increase in the relative number of generalists (GG) and the relative size of the area where they lived. This increase occurred at the cost of the specialist (SS) and intermediate (SG) individuals and eventually resulted in the extinction of the specialist allele S in the metapopulation. We also observed that after a period of temperature increase the relative positions of the SS and GG individuals to the temperature optimum was inversed compared to the positions in the initial distribution (compare in Figure 4.2 the years 400 and 600 with year 0). The generalists occurred at the temperature optimum, where the specialists have a selective

advantage, while the specialists lived at the range margin, where the generalists have a higher fitness. Both effects of inversed positioning and relative increase of generalists were seen under all temperature increase scenarios. The metapopulation only survived under the isocline shift rate of 2 km/year. Under isocline shift rates of 4 km/year and 8 km/year we observed the extinction of the metapopulation before the end of the simulation. With increasing isocline rate shift the extinction of both the S allele and the total metapopulation occurred earlier in time. The level of neutral genetic variation showed a sharp decline in the newly established populations (Figure 4.2) under all temperature increase scenarios.

An increase of the yearly temperature stochasticity to a standard deviation of 280 km, simulating increased temperature variability, resulted in a relative increase of the numbers of the generalist genotype GG compared to the numbers of specialists SS (Figure 4.3). Under range shift this relatively larger fraction of the G allele and/or the relative fitness benefit of the G allele under larger temperature variability led to an earlier extinction of the specialist allele S under range shifts (Figure 4.3). The differences in distributions of the three genotypes in time under range shifts between the levels of temperature variability were similar under all temperature increase scenarios.

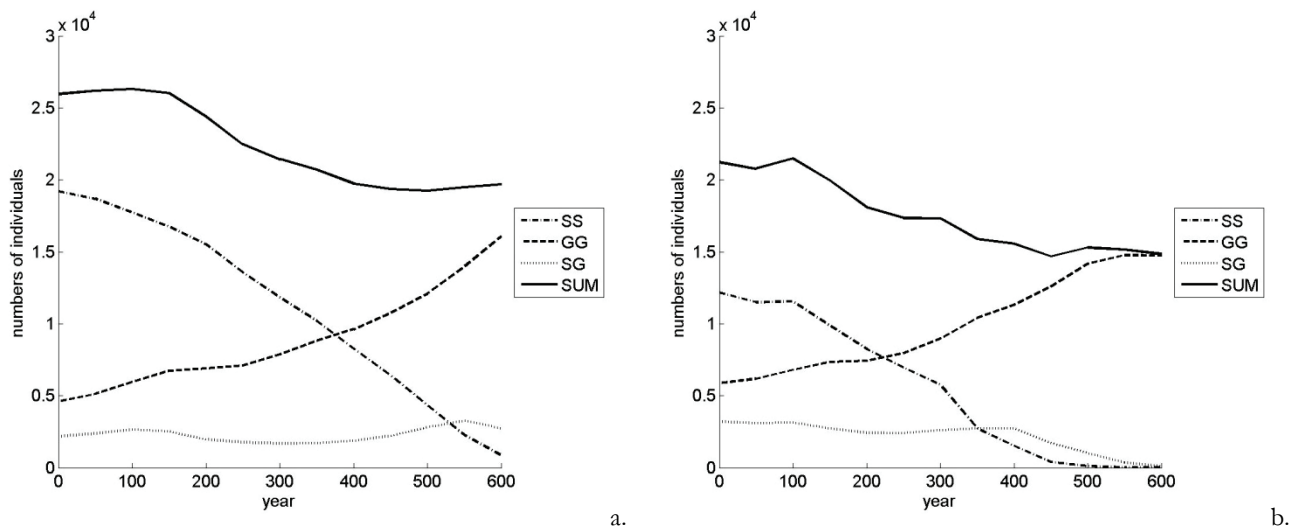


Figure 4.3. The number of generalists (GG), specialists (SS), heterozygotes (SG) and their sum in time under the temperature increase scenario of 2 km/year for standard deviations of 0 km (a) and 280 km (b).

Effects of changing genotype distribution on species' persistence

If the metapopulation was parameterised to contain only S alleles (S-metapopulation) or G alleles (G-metapopulation), its initial size was smaller than when both alleles S and G were present (SG-metapopulation) (Figure 4.4). Under all parameter settings the metapopulation size decreased during a range shift, and the decline of the metapopulation was steepest when it contained both alleles S and G. Compared in time, the size of the SG-metapopulation was at a certain moment smaller than both the S- and the G-metapopulation sizes under the temperature increase scenario of 2 km/year. Under the range shifts induced by the 4 km/year and the 8 km/year scenario, the SG-metapopulation size became smaller than the G-metapopulation but stayed larger than the S-metapopulation. As a result of the gradual decline of the S-allele frequency in the SG-metapopulation under range shift, the sizes of the SG- and G-metapopulations eventually converged under all temperature increase scenarios.

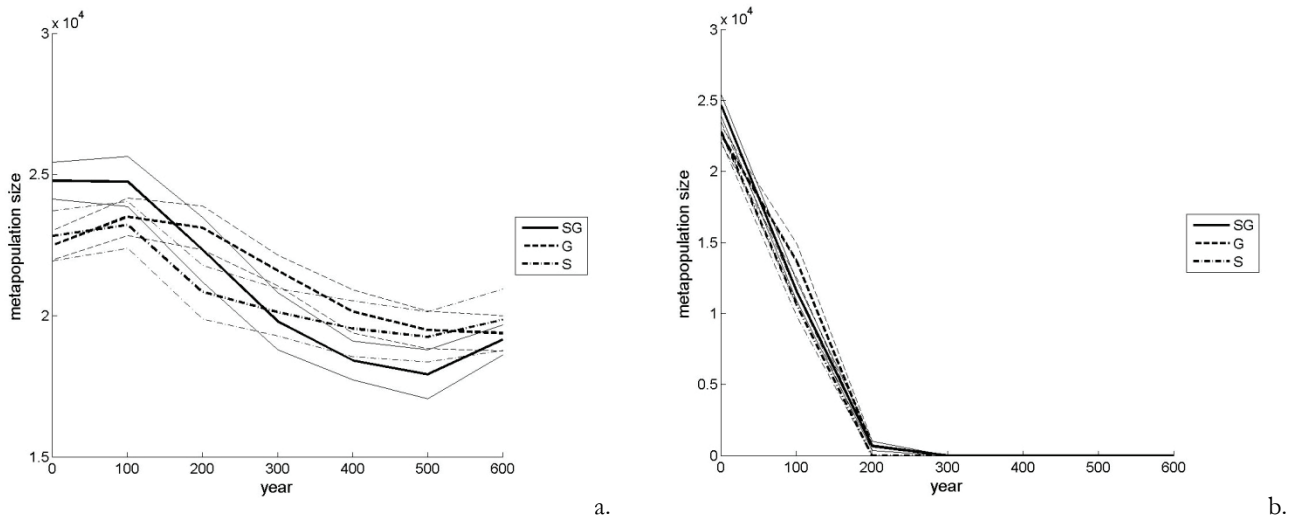


Figure 4.4. The average size and the 95% confidence interval of the metapopulation, which consisted of only the generalist allele (G), of only the specialist allele (S) and of both alleles (SG), under the temperature increase scenario of 2 km/year (a) and 8 km/year (b). Note that the y-axes scales differ.

Recovery of the original genotype distribution after temperature stabilisation

Our model simulations were continued after the implemented temperature increase stopped. In this period the species' range still shifted, until the moment that the metapopulation was distributed evenly again around the temperature optimum. The initial, equilibrium distribution of the SS, SG and GG genotypes in the metapopulation could re-establish itself in three situations, which could occur together:

1. If individuals carrying an S-allele were still present in the area where they have a selective advantage over the individuals with the GG-genotype (Figure 4.5 shows an example). In this case the number of SS and SG individual increased and they moved northwards until they took their initial positions around the temperature optimum. Especially in the 2 km/year scenario recovery was often possible, even after long periods of temperature increase. However, the recovery period always took longer than the period of temperature increase (Figure 4.5).

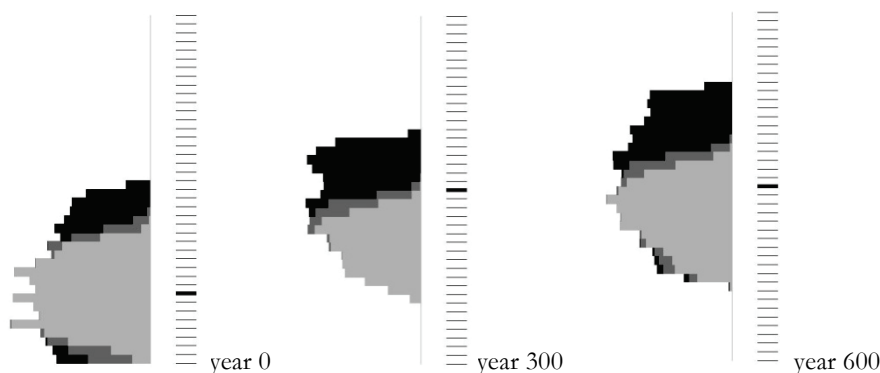


Figure 4.5. The distributions of the GG (black), SG (dark gray), and SS (light gray) genotypes under the temperature isocline shift rate of 2 km/year. The numbers in the lower right corners indicate the years. The bold black bars indicate the locations of the average temperature optimum along the total range of 2000 km. The temperature increase was stopped after 300 years.

2. If a G-allele in the region around the temperature optimum mutated into an S-allele. In this case the individual with this SG-genotype had a selective advantage over the surrounding generalists.

Once this mutation established itself, this led to an increase in the numbers of individuals with the SG- and SS genotypes, until they took their initial positions around the temperature optimum. Such a mutation occurred regularly (in 11 out of 140 runs, for 14 parameter sets) and increased the distribution recovery rate, depending on the time and location of the mutation, compared to the rate without such a beneficial mutation.

3. In the exceptional case of a G-allele mutating into an S-allele at the leading edge of the metapopulation during the range shift (Figure 4.6). In the single example that we detected in our runs, this mutation led to the persistence of the S-allele near the temperature optimum throughout the range shift. In this case, the relative increase of the generalist numbers was limited under range shift.

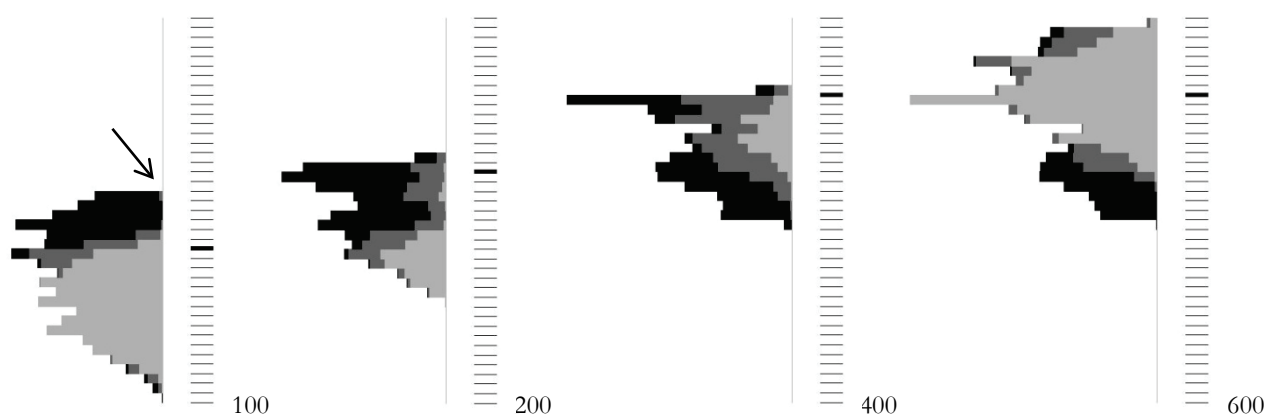


Figure 4.6. The distributions of the GG (black), SG (dark gray), and SS (light gray) genotypes in a single run of the temperature isocline shift rate of 4 km/year. The numbers in the lower right corners indicate the years. The bold black bars indicate the locations of the average temperature optimum along the total range of 2000 km. The temperature increase was stopped after 300 years. In year 100 there were several SG-individuals at the range front, see arrow. These could establish as a result of their selective advantage and were subsequently enhanced by the founder effect, leading to high numbers of specialists and intermediates throughout the range.

DISCUSSION

The purpose of this study was to explore the interaction of local adaptation and founder events under climate change-induced range shifts in response to climate change and its effects on genotype distribution and species' persistence. We found that the distribution of the genotypes in the metapopulation under equilibrium conditions changed when the metapopulation was shifting under temperature increase. This was caused by a founder effect. As a result the genotypes ended up in regions different from those in which they had the highest fitness. This led to a decreased habitat occupancy causing a decreasing metapopulation size and as such impeded species' persistence. This effect was stronger under increased temperature variability.

The results of this study suggest that founder events under range shift in response to climate change may have adverse consequences for species' persistence by impeding local adaptation in newly established populations when these, at a later stage, are located closer to the range centre. Travis *et al.* (2007) showed the possibility of the establishment of deleterious mutations through founder events at expanding range margins. Here we extend their work and show that the enhanced frequency, due to founder events, of the locally best-adapted genotype at the expanding range margin in time had adverse effects on the level of local adaptation throughout the species' range. This occurred despite the fact that

genotypes better-adapted to the range centre were present in the species' range throughout the temperature increase and recovery period.

It has been suggested that local adaptation and range shifts could complement each other, leading to increased species' persistence under climate change (Hoffmann & Sgro 2011, Parmesan 2006). Our study did not provide evidence supporting this suggestion. Instead, we show that range shifts may lead to local maladaptation throughout the species' range and cause decreased species' persistence.

The combined effect of range shift and local adaptation on the genotype distribution in the species range under climate change

As the location of the optimal temperature moved northwards, the suitable climate space for the individuals at the northern range margin of the metapopulation extended northwards as well. The newly available habitat patches became occupied by the generalists living at this northern range edge, accompanied by a clear signature of founder events in the neutral genetic variation (Figure 4.2). In the northern transition area, the changing temperature conditions allowed the individuals carrying the specialist allele S to expand their range as well. However, the expansion of the specialist genotype here was delayed. The observed delay was caused by the absence of the S-allele in the populations where this allele had the selective advantage (as indicated by Figure 4.6), resulting from the founder events. So the habitat sites that the specialist genotype needed to disperse to were already occupied by the climate generalists and, due to their local dominance, most of the dispersers into these populations were generalists too. As a result the establishment rate of the S-allele in these populations to the north of their distribution was not high enough to track the expansion of the generalist populations. Overall, the frequency of the S-allele in populations in the transition region increased, but much slower than the expansion of the generalist range at the northern border of the species' range. Consequently, the size of the northern region where the generalists lived became constantly larger in time, and upon continuing range shift the specialists ended up at the lagging range margin, where generalists were better adapted to the changed climate and therefore performed better. So there the specialist/intermediate populations started to decrease as a result of selection for the better-adapted generalists.

An increased yearly temperature variability led to a further advantage for the climate generalists, because its main effect was a decrease in size of the central part of the range in which the climate specialists could outcompete the individuals carrying a G-allele, so that the initial numbers of climate specialists were lower.

The effect of the changing genotype distribution on the survival of the species

To gain insight into the consequences of the described changes on species' persistence, we compared the size of the metapopulation when it had a mixed allele composition (containing both S and G alleles) with its size when it contained only either the S or G allele.

The initial size of the metapopulation was largest when it contained both alleles. This was presumably the result of the combined local benefits of the present genotypes, overall leading to larger population sizes. Under all parameter settings the metapopulation size decreased during a range shift. This resulted from the inability to use the full potential range to the north of the temperature optimum,

because it took too long to establish new populations in the northern range that became habitable due to a fast shift of the temperature optimum (Schippers *et al.* 2011), even under the slowest temperature increase scenario. However, when the metapopulation contained both alleles S and G it declined most steeply. Under these settings both the specialist and generalist genotypes were living under suboptimal climate conditions, leading to additional loss of individuals in this metapopulation. Counter-intuitively, the decrease of the metapopulation size was only stopped once the specialist allele S went extinct, and the generalists could increase their numbers in the southern part of the species' range.

Recovering the equilibrium genotype distribution after temperature stabilisation

The genetic structure resulting from founder effects under range expansion can be very persistent (Hewitt 1996). Here we show for adaptive genes that the prolonged absence of locally beneficial alleles as a result of founder events may lead to delayed local adaptation. Beneficial mutations can enhance the rate of local adaptation.

Perspectives

The middle spotted woodpecker is a moderate disperser living in fragmented habitat. Bronnenhuber *et al.* (2011) showed in an empirical study that in an invasive fish species founder effects at the expansion front were mitigated through a dual-dispersal strategy which combines both long-distance and contiguous dispersal. This raises the question how species' ecology and the configuration of their habitat may affect the results found in this study and whether our results can be found in empirical studies as well. Nolte (2011) therefore argued for a broader scope of empirical studies with Bronnenhuber *et al.* (2011) as an example.

We modelled genetic differences between central and marginal populations of this species' range. Hoffmann & Blows (1994) concluded in their review that 'marginal populations may often be relatively better-adapted to unfavourable conditions, but perform poorly under most other conditions'. Many species show genetic differentiation between central and marginal populations (Kawecki 2008). Empirical data for our model species the middle spotted woodpecker is lacking on this subject. (Sexton *et al.* 2009) found support for decreasing fitness towards the range margins in half of the reviewed publications, but concluded that evidence for such a generalisation was lacking. However, they did find that 34 out of 43 reviewed papers support the theory that limiting abiotic variables are the cause of a range limit through affected fitness components.

As still little is known about the basis and extent of genetic differentiation between central and marginal populations along an biogeographical gradient, our genetically simple model provides valuable insights into how founder effects under range shifts could interact with local adaptation in species' ranges along such a gradient. It would be very interesting to find out for specific species at specific locations what traits are involved in the differences between centre and range margins and how they are imbedded in the species genome. Detailed simulation models, such as the one used in this study, including species' ecology, genetics and landscape structure, will be useful to explore the variation of persistence probabilities of various species in different habitat configurations.

The examples of mutation establishment that we observed in our results (see Figure 4.6) suggest that the dominance of the GG genotype under range shift might not occur if the initial marginal populations would be genetically more diverse. The chance of a genotype to be enhanced by the founder effect is dependent of its relative fitness (Muenkemueller *et al.* 2011) and its frequency at the ancestral populations. The inclusion of a higher level of polymorphism in the model may lead to genetically more diverse populations in the range margin. A higher level of genetic diversity at the range margin could as well be generated by habitat heterogeneity, which was not included in our model. If this would prevent or hamper founder effects, such a management strategy may be designed to support local adaptation under climate change. To assess whether such a strategy is promising additional modelling and empirical experiments are needed.

APPENDIX 4.1: DETAILED MODEL DESCRIPTION

For this study we used METAPHOR, a simulation model for metapopulation demography (Verboom *et al.* 2001, Vos *et al.* 2001b). The model has been extended to allow for stochastic temperature zone shifts by Schippers *et al.* (2011). Here a new extension provided each individual in this study with an adaptive diploid gene. The yearly metapopulation demography is simulated based on four events: reproduction, dispersal, survival and aging, in this order. Reproduction, dispersal and survival are based on population density and habitat quality. Perceived habitat quality is controlled by time and location specific temperature and the individual's genome. As such we simulate the effect of stochastic temperature zone shifts on the distributions and carrier numbers of the different genotypes in the metapopulation.

Landscape

The landscape we used in the model had dimensions of 15 km from east to west by 2000 km from north to south. The east and west side were merged to create a cylindric landscape. The landscape contained 3000 circular habitat patches of 50 ha each, so consisted of a total of 5% habitat. When generating the landscape, patches were placed in random positions in the landscape, yet only allowed if they were at a minimum distance of 150 m from existing patches. Five landscape variants with different habitat positions were randomly generated in this way.

Climate

Climate is incorporated in the model through habitat quality. Where climate is optimal for the species, habitat quality equals 1, and where climate is unsuitable for the species, habitat quality is 0 (see equation HQ below). Climate change scenarios are based on temperature increase predictions (I °C year⁻¹) by the Hadley Centre of 0.0167 and 0.0333 °C year⁻¹, and we also included a scenario with a temperature increase of 0.084 °C year⁻¹. Besides, the used scenarios include weather variability increase assumptions as temporal stochasticity in the temperature (the current standard deviation of the average temperature σ_t (°C), 0.59 °C (Schippers *et al.* 2011). Climate in our model is thus defined as the temperature in year t and at location Y . Climate change is then the speed with which temperature isoclines travel north (T km year⁻¹) and the yearly fluctuation of these lines (σ_d km). We use a climatic gradient from south to north of G (°C km⁻¹) to get to:

$$T = I / G, \text{ and}$$

$$\sigma_d = \sigma_t / G$$

This results in a current yearly fluctuation of the temperature isoclines σ_d of 140 km, and we further included scenarios with yearly fluctuations σ_d of 0 km and 280 km. We can then calculate the location of the optimal temperature in north-south direction (Y_{opt}) in a certain year as:

$$Y_{opt,t} = Y_{opt,0} + T * t + \sigma_d * N_t$$

with N_t is the yearly random number drawn from a standard normal distribution.

We obtain a normal habitat quality distribution with this optimal coordinate Y_{opt} in its centre by defining habitat quality (HQ) as

$$HQ_{patch, t, ind} = HQfactor_{gen} * \exp[-0.695(Y_{opt,t} - Y_{patch})^2 / H_{gen}^2]$$

H_{gen} is an indicator of the temperature tolerance of the specific genotype, and defined as the distance from the temperature optimum at which habitat quality is 0.5. See Table 4.1. $HQfactor_{gen}$ determines the perceived habitat quality of the individual with its specific genotype. This factor serves as a trade-off for the larger temperature tolerance of the climate generalist genotype GG.

Species

We modelled a woodland bird, parameterised as the middle spotted woodpecker (*Dendrocopus medius*). Parameters were based on biological information (Hagemeijer & Blair 1997, Kosenko & Kaigorodova 2001, Kosinski *et al.* 2004, Kosinski & Ksit 2006, Michalek & Winkler 2001, Pasinelli 2000, Pettersson 1985a, Pettersson 1985b) and on the interpretation by Schippers *et al.* (2011) (see Table 4.1). The model distinguishes 2 sexes and 2 life stages: adults and juveniles. The yearly life cycle consists of recruitment, dispersal, and survival, in this order. Lastly, all juveniles age to adults. Recruitment, dispersal and survival are all dependent of life stage, population density (PD) and habitat quality (HQ).

$$PD = N_t / CC,$$

with N_t : number of individuals in patch,
 CC : carrying capacity of patch, and
 HQ : see section Climate in this appendix.

Species: recruitment function

The number of nests in a patch in each generation is equal to the number of unique adult pairs of opposite sex in this patch, with a maximum of 10. The number of offspring per nest is then found with:

$$N_o = N_{O_PD_0HQ_1} * \left(1 - \left(1 - \frac{N_{O_PD_0HQ_0}}{N_{O_PD_0HQ_1}}\right) * (1 - HQ)\right) * \left(1 - \left(1 - \frac{N_{O_PD_1HQ_1}}{N_{O_PD_0HQ_1}}\right) * PD\right)$$

with $N_{O_PD_0HQ_1}$: number of offspring at population density (PD) = 0 and habitat quality (HQ) = 1, and similar for $N_{O_PD_0HQ_0}$ and $N_{O_PD_1HQ_1}$. See Table 4.1.

Species: survival function

Determines for each individual the chance that it survives the current year, P_S .

$$P_S = P_{S_PD_0HQ_1} * \left(1 - \left(1 - \frac{P_{S_PD_0HQ_0}}{P_{S_PD_0HQ_1}} \right) * HQ \right) * \left(1 - \left(1 - \frac{P_{S_PD_1HQ_1}}{P_{S_PD_0HQ_1}} \right) * (1 - PD) \right)$$

with $P_{S_PD_0HQ_1}$: survival rate at population density (PD) = 0 and habitat quality (HQ) = 1, and similar for $P_{S_PD_0HQ_0}$ and $P_{S_PD_1HQ_1}$. See Table 4.1.

Species: dispersal function

Determines for each individual the yearly chance that it leaves its patch to go on dispersal, P_D .

$$P_D = P_{D_PD_1HQ_1}(-1 + HQ + PD) + P_{D_PD_1HQ_0}(1 - HQ) + P_{D_PD_0HQ_1}(1 - PD)$$

with $P_{D_PD_1HQ_1}$: dispersal rate at population density (PD) = 1 and habitat quality (HQ) = 1, and similar for $P_{D_PD_1HQ_0}$ and $P_{D_PD_0HQ_1}$. See Table 4.1.

If an individual disperses, we need to determine where it goes. From their origin patch individuals can go in every direction, along a straight line. Connectivity to other patches is determined by destination patch radius (r) and distance to there (d). So the chance to disperse from patch A to patch B is:

$$P_{AB} = \frac{2 * \arcsin\left(\frac{r_B + l}{d_{AB}}\right)}{2\pi}$$

with l is 150 m, the maximum distance from where an individual can detect suitable habitat. The maximum dispersal distance is 15 km, so habitat patches that are separated by more than this distance are not connected at all. Our model does not allow dispersers to ignore a nearer patch, so more distant patches are located in the shadow of the nearer patch. An individual may arrive in a patch with a population size larger than carrying capacity twice per dispersal event, and is then allowed to disperse again. Should it fail to reach a habitable patch within a total of three dispersal rounds, it dies.

Initialisation

At initialisation of the model, all habitat patches were filled with 10 adult individuals, equaling half the carrying capacity. Each individual was randomly given 2 alleles. The climate optimum Y_{opt} was initialised at 400 km from the southern landscape edge.

Burn-in

After initialisation the model was run for 3000 generations, thus 3000 years. During these 3000 years burn-in, the model runs with temperature isocline speed T equaling 0 in the equation for $Y_{opt,t}$. After this burn-in we started our experiments.

Experiments

In the experiments the temperature isoclines were simulated to move northward for 600 years, under the different scenarios in Table 4.1. Each parameter setting was run twice in each landscape variant (10 runs in total). For studying trends in numbers of individuals we averaged these per parameter setting.

CHAPTER FIVE

INCREASED DISPERSAL UNDER CLIMATE CHANGE-INDUCED RANGE SHIFTS IN A FRAGMENTED HABITAT: A KEY ROLE FOR FOUNDER EFFECTS

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ABSTRACT

Many species are shifting their ranges under contemporary global warming. There is increasing evidence for the evolution of dispersal capacity in populations at the expanding margins of such ranges. Range shifts also cause founder events, which can affect the evolutionary process in these populations. With a simulation model we observed that local adaptation for increased dispersal probability under range shift was greatly enhanced by founder events that exclusively promoted the fast-dispersing alleles. This impeded subsequent population adaptation under changing selective pressure at a later stage, as dispersal rate remained high even when this was not optimal. It has been suggested that there is a positive feedback between range expansion and the evolution of traits that accelerate range expansion. We underline the existence of such a feedback, but add that this loop may be enhanced by founder events, with adverse effects on species' survival in the long term.

INTRODUCTION

Climate change is considered a threat to biodiversity as species that do not respond adequately to the changes in their environment may go extinct. One response to climate change, which has been observed for many species around the world, is a shift of range as species track their preferred temperatures polewards or to higher elevation (Chen *et al.* 2011, Parmesan & Yohe 2003, Root *et al.* 2003). The speed with which a species can shift its range is determined by its dispersal capacity in interaction with other life history traits and the level of fragmentation of its habitat (Opdam & Wascher 2004, Schippers *et al.* 2011, Travis 2003). To disperse is potentially advantageous for an individual because it allows escape from competition (Ronce 2007). At the same time dispersal is a risky activity as it implies increased mortality (Ronce 2007). When a species' range coincides with an ecological gradient, such as a temperature gradient, the habitat sites along this gradient become increasingly less suitable (Kawecki 2008). In the margins of the range, site conditions may temporarily exceed the species' tolerances (Sexton *et al.* 2009), causing relatively low population density and habitat occupancy compared to habitat sites central in the species range (Kawecki 2008). From an evolutionary point of view, the relative benefit of dispersal is therefore expected to be larger in the range margins than in the centre of the range (Ronce 2007, Sexton *et al.* 2009, Southwood 1962), and we can expect directional selection for increased dispersal in the margins (Sexton *et al.* 2009). In the centre of the range, the relative fitness of an individual with a particular dispersal capacity depends on the frequencies of the other levels of dispersal capacity, and frequency-dependent selection is expected (Ronce 2007) towards a combination of different dispersal capacities. The resulting equilibrium combination of dispersal capacities will depend of the level of variability of the local environment (Comins *et al.* 1980), and may vary across the range.

Under contemporary global warming, with changing conditions that permit the expansion of the species range into regions that previously were too cold, one may expect further selection for increased dispersal capacity. Evolution towards increased dispersal capacity at the expanding front of shifting populations has indeed been found in many studies, both theoretical and empirical (reviews by Hill *et al.* 2011, Ronce 2007). Hill *et al.* (2011) suggest that there is a positive feedback between range expansion and the evolution of traits that accelerate range expansion. This positive feedback is expected to increase species' survival under global climate change (Hoffmann & Sgro 2011, Parmesan 2006).

However, Klopstein *et al.* (2006) and Travis *et al.* (2007) show in model simulations that range expansions can also cause genetic and evolutionary changes as a result of founder events. This is due to the demographic advantage of an allele which is first to arrive in an empty habitat patch at an expanding range front compared to others arriving later. Travis *et al.* (2007) shows that this could even lead to the establishment of a deleterious mutation in the newly colonised area. In contrast, Cobben *et al.* (this thesis, Chapter 4) observed founder events to enhance local adaptation in newly established populations under range shift. When the selective pressure changed at a later stage, these populations however experienced delayed adaptation as a result of the genetic impoverishment caused by these founder events.

Observed increases in local frequencies of genotypes with better dispersal capacities at expanding range margins may thus be caused by local adaptation, but could also be affected by founder events. It is of crucial importance to understand the relative effect of adaptation and founder events, because of the potential adverse consequences of the founder effect. However, while founder effects have been clearly associated with the patterns in neutral genetic diversity observed after range expansions (Excoffier *et al.* 2009, Garroway *et al.* 2011, Hewitt 1996), studies showing trait evolution under range shifts have thus far not investigated the potential role of founder effects. In this paper we explore whether founder events can contribute to the increased dispersal at expanding range margins, and study the consequences of such a contribution.

We simulated a metapopulation of middle spotted woodpecker (*Dendrocopos medius*) in which individuals had different alleles for dispersal probability. Consistent with current insights as summarized above, we expected frequency-dependent selection in the centre of the range, and selection for increased dispersal near the range margins, with overall higher levels of dispersal probability with increasing temperature variability. The metapopulation was then subjected to three temperature increase scenarios (HadleyCentre 2003, Schippers *et al.* 2011). We studied how the distribution of the different genotypes changed under different scenarios of temperature increase and in the period after the temperature had stabilised again. To disentangle founder effects from selection, we also ran the model with fixed allele compositions, and with all alleles present in equal proportions.

METHODS

For this study we used METAPHOR, a simulation model for metapopulation demography (Verboom *et al.* 2001, Vos *et al.* 2001b). The model has been extended to allow for a gradual temperature increase with a large stochasticity from year to year by Schippers *et al.* (2011). It received a module for neutral genetic diversity (Cobben *et al.* 2011). Here we further extended the model with a genetic module for adaptive traits. Survival and reproduction were based on population density and habitat quality. The habitat quality was controlled by the time and location specific temperature. The individual's dispersal probability depended on its genotype. Through the feedback loop of reproduction and survival the selection for a certain dispersal allele was dependent of the local temperature, which increased with a large stochastic component. In this way we simulated the effect of climate change on the spatial distribution of the different dispersal probability genotypes in a metapopulation under range shift. For detailed information see Appendix 5.1. Table 5.1 gives an overview of all species, gene and climate parameters used.

The landscape we used in the model had dimensions of 15 km from east to west by 2000 km from north to south. The east and west side were merged to avoid edge effects, creating a cylindric landscape. The landscape contained 3000 circular habitat patches of 50 ha each, so consisted of a total of 5% habitat. Patches were placed in random positions in the landscape, yet only allowed if they were at a minimum distance of 150 m from existing patches. Five landscape variants with different habitat positions were randomly generated and each simulated parameter setting was repeated twice in each landscape variant.

Table 5.1. Model parameters used. *HQ* means habitat quality and *PD* is population density. Parameter names link this table to the functions in Appendix 5.1: Detailed model description.

Parameter description	Value	Unit	Parameter name
Landscape parameters			
number of patches	3000		
patch area	50	ha	
patch carrying capacity	20	individuals	
Species parameters			
<i>Recruitment</i>			
area per reproductive unit	5	ha	
recruitment at density = 0 and quality = 1	2.4	juveniles/female	N_{O_PD0HQ1}
recruitment at density = 1 and quality = 1	1	juveniles/female	N_{O_PD1HQ1}
recruitment at density = 0 and quality = 0	0	juveniles/female	N_{O_PD0HQ0}
<i>Dispersal</i>			
maximum dispersal distance	15	km	
maximum detection distance	150	m	l
dispersal probability genotype AA	0.0	year ⁻¹	P_{D_GEN}
dispersal probability genotype AB	0.1	year ⁻¹	P_{D_GEN}
dispersal probability genotype BB	0.2	year ⁻¹	P_{D_GEN}
dispersal probability genotype BC	0.3	year ⁻¹	P_{D_GEN}
dispersal probability genotype CC	0.4	year ⁻¹	P_{D_GEN}
dispersal probability genotype CD	0.5	year ⁻¹	P_{D_GEN}
dispersal probability genotype DD	0.6	year ⁻¹	P_{D_GEN}
dispersal probability genotype DE	0.7	year ⁻¹	P_{D_GEN}
dispersal probability genotype EE	0.8	year ⁻¹	P_{D_GEN}
dispersal probability genotype EF	0.9	year ⁻¹	P_{D_GEN}
dispersal probability genotype FF	1.0	year ⁻¹	P_{D_GEN}
<i>Survival</i>			
juvenile survival probability	1	year ⁻¹	P_{S_PD0HQ1} , P_{S_PD1HQ1} , P_{S_PD1HQ0}
juvenile survival standard deviation	0.15	year ⁻¹	σ_s
adult survival probability at HQ=1, PD=1	0.6	year ⁻¹	P_{S_PD1HQ1} ,
adult survival probability at HQ=1, PD=0	0.8	year ⁻¹	P_{S_PD0HQ1}
adult survival probability at HQ=0, PD=1	0.35	year ⁻¹	P_{S_PD1HQ0}
adult survival standard deviation	0.15	year ⁻¹	σ_s
Genetic parameters			
allele range at initialisation	A-F		
allele range after mutation	A-F		
mutation rate	10 ⁻⁶	generation ⁻¹	
Climate parameters			
temperature isocline speed	2, 4, 8	km year ⁻¹	T
weather variability	0, 140, 280	km	σ_d
temperature tolerance	600	km	H
initial temperature optimum location	400	km from the south edge	$Y_{opt,0}$
Model run parameters			
burn-in	500	years	

We modelled a woodland bird, parameterised as the middle spotted woodpecker (*Dendrocopos medius*). Parameters were based on biological information (Hagemeijer & Blair 1997, Kosenko &

Kaigorodova 2001, Kosinski *et al.* 2004, Kosinski & Ksit 2006, Michalek & Winkler 2001, Pasinelli 2000, Pettersson 1985a, Pettersson 1985b) and on the interpretation by Schippers *et al.* (2011) (see Table 5.1). The model distinguished two sexes and two lifestages. Recruitment and survival were all dependent of population density and habitat quality. From their origin patch individuals could disperse in every direction, along a straight line. Connectivity to other patches was determined by destination patch radius and by distance from original to destination patch. The maximum dispersal distance was 15 km, so habitat patches that were separated by more than this distance were not directly connected. Our model did not allow dispersers to ignore a nearer patch, so more distant patches were located in the shadow of the nearer patch. An individual may arrive in a patch with a population size larger than carrying capacity twice per dispersal event, and was then allowed to disperse again. If it failed to reach a habitable patch within three dispersal rounds, it would die.

The temperature optimum was shifting northwards according to the temperature increase scenario used (see below and Table 5.1). The temperature variability was simulated by the standard deviation of the average temperature (see below and Table 5.1). Climate suitability was translated to a habitat patch quality ranging from 0 to 1, based on distance from the climate optimum and on the half value parameter used, following a Gaussian curve (Schippers *et al.* 2011). We used three temperature increase scenarios, based on work by the Hadley Centre (2003). The first scenario was a temperature increase of 1 °C from year 2000 to 2100. For as far as we know now, this is an unrealistic prediction for the coming century but we incorporated it as an absolute minimal change to compare with the more likely scenarios of a 2 °C and 4 °C temperature increase by 2100 (HadleyCentre 2003). When translating these scenarios to temperature isocline shift rates we assumed that the simulated metapopulation was situated along the European Atlantic coast. Unaffected by mountain ranges it has a temperature gradient of 0.0042 °C per km (Schippers *et al.* 2011). The three scenarios were therefore equivalent to isocline shift rates of respectively 2, 4 and 8 km per year. The current standard deviation of the average temperature is 0.59 °C. We translated this into a distance as well, so in our model the temperature variability was a random variation in the location of the optimal temperature to the north or to the south with a standard deviation of 140 km (Schippers *et al.* 2011). The effect of the temperature variability was assessed by additionally applying standard deviations of 280 km and 0 km.

The model was built to accommodate all dispersal probabilities from 0% to 100%. For this, six alleles existed at one locus for dispersal probability (DP), named A-F, which represented dispersal probabilities of 0%-100% in steps of 20%. The species is diploid, with two alleles at this locus in each individual bird, so 6 homozygote (AA, BB, .., FF) and 15 heterozygote (AB, AC, ..) genotypes were possible. There was codominance between alleles and the dispersal probability of a heterozygote was the average of that of its two alleles, so an individual with genotype AB had 10% probability to disperse (we call this 10% DP). The alleles could mutate into a randomly chosen other allele with frequency 10^{-6} (Nachman & Crowell 2000). We initialised the model with 30 000 individuals, which were randomly given 2 alleles of any of the alleles A, B or C, so the initial metapopulation consisted of individuals with dispersal probabilities of 0%, 10%, 20%, 30%, and 40% dispersal probability (DP). After initialisation we simulated 500 generations to obtain an equilibrium situation. During these 500 generations, there

was no temperature increase in the model, but the simulated yearly stochastic temperature variation was already present. In the remainder of the paper, time 0 is set after this burn-in phase of 500 generations.

Simulation experiments

In this study we did four different model experiments.

1. We investigated the effects of temperature increase and variability on the spatial distribution of the genotypes. For this we assessed the numbers and spatial distributions of the different dispersal genotypes in time under nine climate change scenarios. The temperature isoclines were simulated to move northward for 500 years according to the three temperature isocline shift scenarios of 2 km/year, 4 km/year and 8 km/year. For each of these we additionally varied the yearly stochastic temperature variability by using standard deviations of 0 km, 140 km, and 280 km of the temperature optimum.

2. We looked into the recovery of the original distributions of dispersal probability genotypes after a period of range shift caused by the three rates of temperature increase, with a standard deviation of 140 km. For this we stopped the temperature increase and thereafter continued the simulation for another 300 years.

3. To assess the relative fitness of the dispersal probability (DP) genotypes under temperature increase, we observed the fluctuations in the sizes of metapopulations with different, but fixed, dispersal probabilities under the three temperature increase scenarios, with the yearly temperature variation of the range optimum at a standard deviation of 140 km. In these metapopulation variants the dispersal probability genotype was fixed at 0%DP, 10%DP, 20%DP, 30% DP and 40% DP, with no possibility of mutation. The sizes of the metapopulations in these runs were compared, taking the metapopulation size as a proxy of relative fitness of the dispersal probability genotypes under temperature increase.

4. To assess the relative importance of the founder effect on the frequency increase of the fittest genotype, we neutralised the influence of the founder effect on the outcome of the simulations in experiment 1. For this we repeated the simulations of experiment 1, but without burn-in phase. When omitting the burn-in phase, the temperature increase is implemented immediately after the initialisation of the model. At initialisation the allele frequencies throughout the metapopulation were equal, so the dispersal probability genotypes at the expansion front were present at the expected frequencies under random mating, without a frequency advantage of the locally best-adapted genotype.

RESULTS

Effects of temperature increase and variability on the spatial distribution of the genotypes

After the burn-in phase, so under equilibrium conditions, the metapopulation consisted of individuals with 0%, 10% and 20% DP (genotypes AA, AB and BB; Figure 5.1 year 0). All three genotypes were present in the total range but the 0% DP individuals dominated the centre of the range, while 20% DP individuals had the highest frequency in the margins, where habitat quality and population density were generally lower. The 10% DP individuals took an intermediate position. Under higher yearly temperature variability, the relative frequency of the 20% DP individuals increased throughout the

range (see Figure 5.2a and b at year 0). The original distribution of the genotypes in the metapopulation changed under the range shift which was induced by the temperature increase (see Figure 5.1 year 0). This led to an increase of the proportion of 20% DP individuals and the size of the area where they lived, at the leading edge of the metapopulation. This increase occurred at the expense of the 10% DP and 0% DP individuals and eventually resulted in the extinction of the A allele in the metapopulation. With increased temperature variability this occurred earlier in time (see Figure 5.2). We also observed that after a period of temperature increase the position of the 0% DP individuals shifted to the range margin at the lagging edge compared to its central position in the initial distribution (see Figure 5.1 year 500). In all three scenarios the metapopulation size declined under temperature increase and in the 4 km/year and 8 km/year scenarios it went extinct before the end of the simulation. The rate of decline was larger under increased yearly temperature variability (see Figure 5.2). We did not see the establishment of higher dispersal probability genotypes, not even under large temperature increase or variability. Mutations did lead to the appearance of 30% DP (genotype BC) individuals, which survived and reproduced for some time (see the occasional appearances of the ‘rest’ line at the 0-axis of Figure 5.2), but they always disappeared again after a couple of generations.

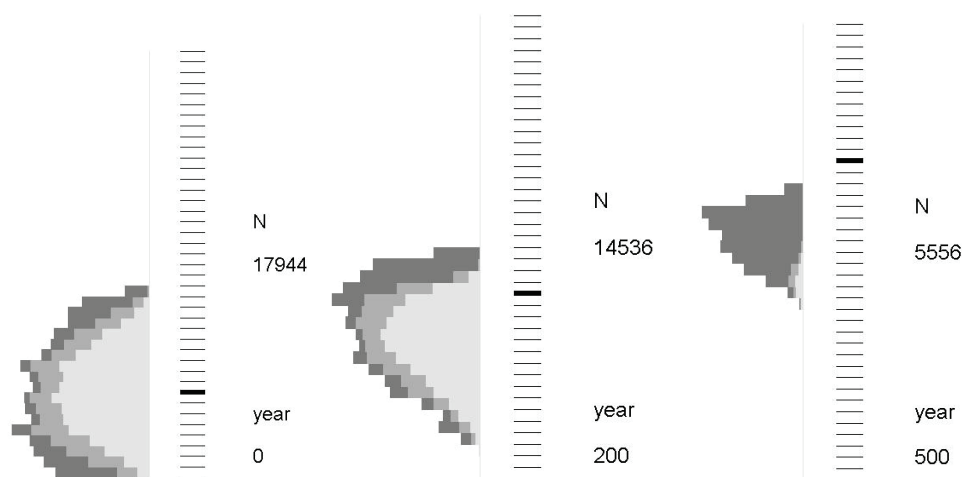


Figure 5.1. The distributions of the 0%DP (light grey), 10%DP (darker grey), and 20%DP (darkest grey) individuals in time in the landscape under the range shift caused by the temperature isocline shift rate of 2 km/year. The standard deviation of the location of the temperature optimum was 140 km. The N numbers give the total size of the metapopulation. The bold black bars indicate the locations of the average temperature optimum along the total range of 2000 km in the specific years.

Recovery of the initial genotype distribution after a period of temperature increase

Under certain conditions the initial, equilibrium distribution of the 0%DP, 10%DP and 20%DP genotypes in the metapopulation could re-establish itself after the temperature increase had stopped (Figure 5.3). This occurred only as long as the 0%DP individuals were still present near the range centre, where they are the best-adapted, at the time that the temperature stabilised. In this case their frequency increased and they eventually recovered their original dominant position in the range centre. However, the period of recovery always took longer than the period during which the temperature increased. This recovery period further increased with a higher rate of temperature increase and with a

longer duration of the increase period. During the recovery period, the 20%DP individuals dominated the metapopulation.

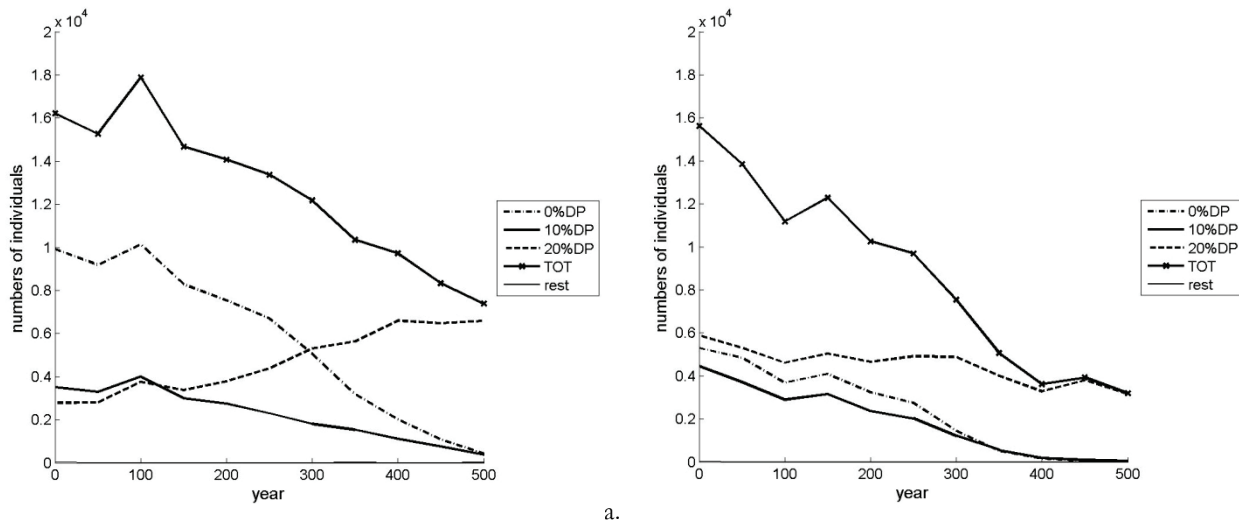


Figure 5.2. The number of 0%DP, 10%DP, 20%DP and the other (30%DP-100%DP) individuals (rest) and their sum (TOT) in time under the temperature increase scenario of 2 km/year for yearly temperature variabilities of 0 km (a) and 280 km (b).

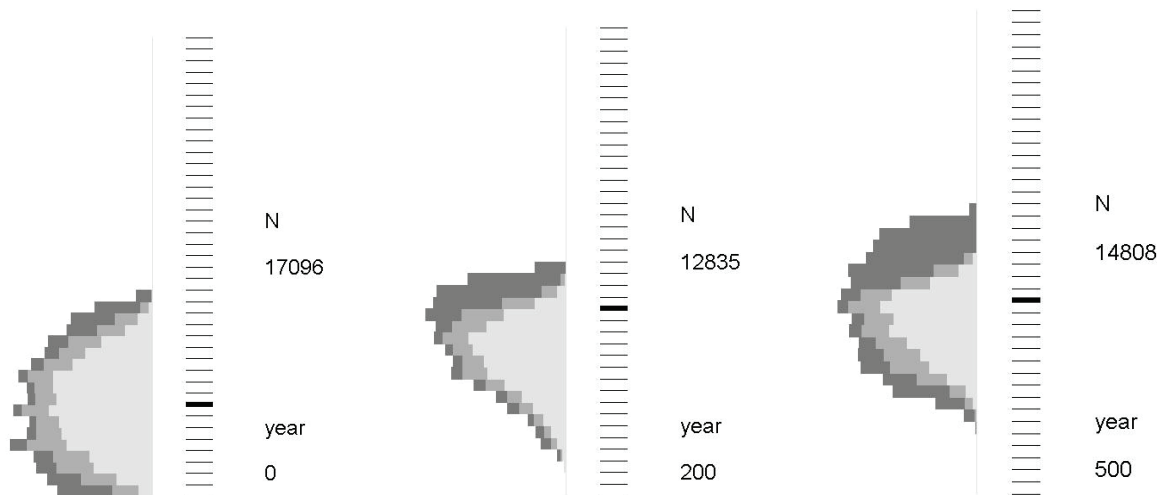


Figure 5.3. The distributions of the 0%DP (light grey), 10%DP (darker grey), and 20%DP (dark grey) individuals in time under the range shift caused by the temperature isocline shift rate of 2 km/year. The temperature variability was set at the current rate (standard deviation 140 km). After 300 years the temperature increase was stopped. The N numbers give the total size of the metapopulation. The bold black bars indicate the locations of the average temperature optimum along the total range of 2000 km in the specific years.

The relative fitness of the different genotypes under temperature increase

We simulated several metapopulations which were fixed for various dispersal probabilities and compared their sizes with that of the metapopulation containing all dispersal probability genotypes (all-DP). At initialisation the size of the all-DP metapopulation was the largest (see Figure 5.4a, TOT-line), but very similar to the size of the metapopulation only 10%DP individuals (see Figure 5.4b, 0.1-line). Under temperature increase the sizes of all metapopulations decreased, and after 500 years the size of the 20%DP metapopulation was the largest. The 10%DP curve showed the highest rate of decline. The size of the 0%DP metapopulation was very small compared to the others, even though they dominated the all-DP metapopulation before the range shift.

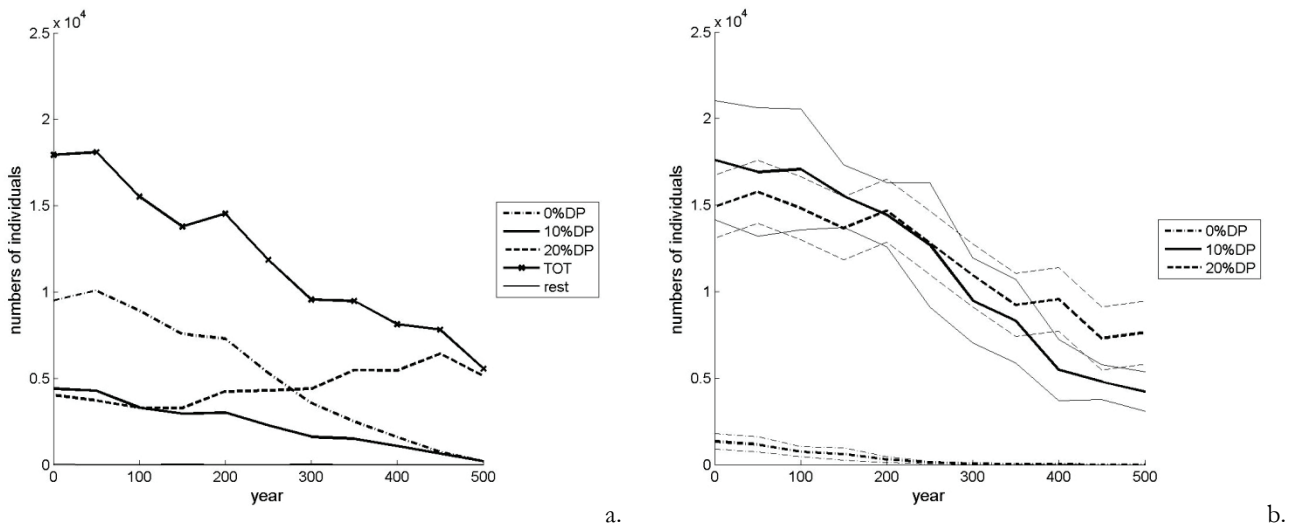


Figure 5.4. (a) The size of the metapopulation consisting of all genotypes, all-DP (TOT), split into numbers of 0%DP, 10%DP, 20%DP and all other individuals (30%DP-100%DP) (rest). (b) The sizes of five metapopulations, each consisting only of individuals with the same single dispersal probability, from 0%DP to 40%DP. Both figures show sizes in time under the temperature increase scenario of 2 km/year and yearly weather variability of 140 km.

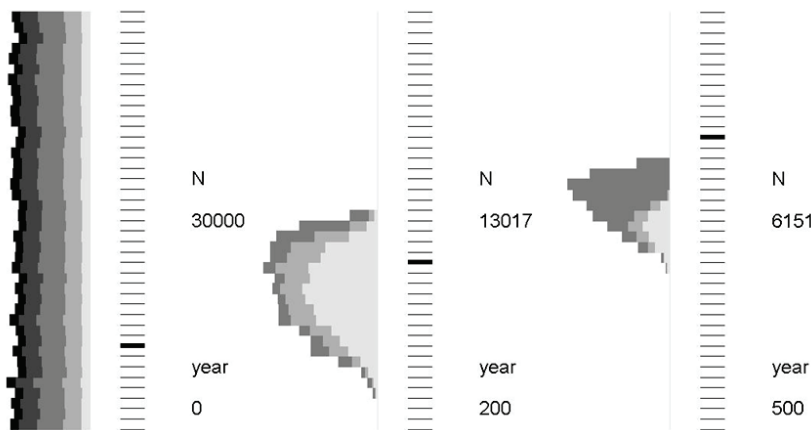


Figure 5.5. The distributions of the 0%DP (lightest gray), 10%DP (light gray), 20%DP (dark grey), 30%DP (darkest gray), and 40%DP (black) individuals in time under the range shift caused by the temperature isocline shift rate of 2 km/year, in a model simulation without burn-in phase. The yearly standard deviation of the optimum temperature location was 140 km. The N numbers give the total size of the metapopulation. The bold black bars indicate the locations of the average temperature optimum along the total range of 2000 km at the specific time points.

The relative importance of the founder effect for the frequency increase of the 20% dispersal probability individuals under range expansion

In the simulations without burn-in phase the three dispersal probability alleles A, B, and C started out at equal frequencies. Under random mating the relative frequencies of the AA, AB, AC, BB, BC, and CC genotypes were 1:2:2:1:2:1 at initialisation and as a result the relative frequencies of the 0%DP, 10%DP, 20%DP, 30%DP, and 40%DP phenotypes were 1:2:3:2:1 throughout the whole species' range, including the northern range margin. With these initial conditions we observed an increase in the frequency of the 20%DP individuals, mainly at the cost of the frequencies of the 30%DP and 40%DP individuals (Figure 5.5), under all temperature increase scenarios. Compared to the simulations that did include a burn-in phase, the persistence of the 0%DP and 10%DP individuals increased. In Figure 5.1

we can see a retraction of these individuals from the northern range margin in year 200, which is not the case in Figure 5.5. When comparing year 500 we clearly see a difference between Figure 5.1, including a founder effect that benefits the 20%DP individuals at the range margin, and Figure 5.5, in the form of persisting numbers of the 0%DP (five times more) and 10%DP (three times more) individuals.

DISCUSSION

The purpose of this study was to investigate the interaction of founder effects and the local adaptation of dispersal probability in response to climate change. We aimed to get insight into the potential role of founder events in the observed increased dispersal capabilities at the expanding margins of species ranges in several studies (see review by Hill *et al.* 2011), by disentangling these separate processes.

The equilibrium distribution of the dispersal probabilities featured a larger dispersal probability at the range margins, compared to the centre of the range, and overall higher dispersal probability under increased yearly temperature variability (consistent with Comins *et al.* 1980, Southwood 1962). Under various scenarios of temperature increase and in the period after the temperature had stabilised again, the high, i.e. 20%, dispersal probability individuals dominated the newly established populations beyond the original range limit. A comparison of the sizes of the single genotype metapopulations indicated that these 20% dispersal probability individuals were most fit under temperature increase. On top of this, when comparing Figure 5.3a with 5.3b it became clear that a metapopulation consisting of only 20% dispersal probability individuals performed better than the metapopulation with various dispersal probabilities in which selection for such 20% dispersal probability individuals was taking place. This indicates that the increasing dominance of 20% dispersal probability individuals in that metapopulation was beneficial for the metapopulation survival. However, after neutralising the founder effect we assessed that the increase in frequency of this beneficial genotype had been greatly enhanced by the founder effect. In the short term the founder effect thus contributed to a fast increase of the most adapted allele. However, the additional loss of genetic diversity caused by the founder effect meant that other alleles were absent, which impeded the local adaptation of the populations established beyond the original range limit at a later stage, when these populations gradually came closer to the range centre and frequency-dependent selection towards a combination of dispersal genotypes (including a large proportion of zero dispersal probability individuals) was to be expected.

Hill *et al.* (2011) suggested that there is a positive feedback between range expansion and the evolution of traits that accelerate range expansion. Here we show three important characteristics for dispersal probability in the range margins. First, such accelerating genotypes are likely to be dominant at the range margins prior to temperature increase. Second, local adaptation towards increased frequencies of such genotypes in newly established populations under range expansion is therefore likely to be greatly enhanced by founder events, which is further supported by Muenkemüller *et al.* (2011) who showed in a modelling study that the average frequency of a mutation in a newly established population under range shift increases with its fitness. Third, this founder effect counteracts the frequency increase of lower dispersal probability genotypes in these populations later in time, when they become located

nearer to the species' range centre. We thus agree with Hill *et al.* (2011) that such a positive feedback exists, but add that this loop may be enhanced by founder events, which may cause adverse effects on population and species' survival at a later stage.

Dispersal probability distribution under equilibrium conditions and increased temperature variability

Under the equilibrium situation the distribution of the dispersal probabilities concurred with the expectations of Sexton *et al.* (2009). With increased yearly temperature variability a higher dispersal probability became increasingly advantageous throughout the range, as expected by theory (Comins *et al.* 1980). The single genotype simulations showed that metapopulations consisting solely of individuals with zero dispersal probability hardly survived the current temperature variability (see Figure 5.3b). However dominant these individuals were around the range centre, they needed some dispersing individuals to overcome occasional population extinctions due the climate stochasticity. After such an extinction, a habitat site was recolonised by dispersing individuals. Once this site showed more or less stable quality for a certain period, re-appearing individuals with zero dispersal probability had the selective advantage and re-established themselves. So besides the spatial selection differentiation between species' range centre and margins, there was also a temporal selection differentiation, with directional selection for increased dispersal probability after a population extinction and frequency-based selection once the new population was established. Similar differences between new and old populations were shown by Hanski *et al.* (2004). Increased yearly temperature variability changes the stability of the populations, leading to higher local extinction and recolonisation rates, so there are more relatively new populations and individuals with a higher dispersal probability have a higher relative fitness. The consequence is a lower overall population size, leading to an increased metapopulation extinction probability.

Changing genotype frequencies under temperature increase

With increasing temperature the metapopulation started to shift its position in the landscape, but at a rate too slow to keep track with the optimal temperature, even under the slowest temperature isocline movement. The individuals with high dispersal probability colonised all the habitat patches to the north of the metapopulation. Later on the habitat quality increased as a result of the increasing temperature. As the metapopulation kept shifting, the populations of individuals with lower dispersal probabilities were pushed backwards towards the southern range margin, where they were not selectively advantageous and suffered from accelerated decline. At a certain point in time the distribution of dispersal probabilities was exactly the opposite as would be selectively optimal (e.g., Figure 5.1 after 500 years, high dispersers in the centre and low and zero dispersers at the range margin).

Thus, the increased frequency of 20% dispersal probability individuals was beneficial for the metapopulation survival during temperature increase as was indicated by the relative sizes of the single genotype metapopulations, and by the relative increase of 20% dispersal probability individual numbers in the simulations with the neutralised founder effect. However, in these simulations we also observed an increased persistence of the lower dispersal probability individuals under temperature increase, which we did not observe in the normal runs. This means that the frequency increase of the good

dispersers in the normal runs was not solely the result of local adaptation but was enhanced by repetitive founder events. We therefore conclude that the increased dispersal in the new populations established during range shift induced by temperature increase, was the result of both founder effect and local evolution towards more beneficial genotypes.

Changing genotype frequencies after stabilisation of the temperature

Although the selection for the highly dispersive individuals at the expanding range margin was beneficial for the metapopulation survival under climate change, these populations were subjected to a frequency-based selection towards a combination of zero, low and higher dispersal probability individuals as they grew older (cf Hanski *et al.* 2004) when they became located nearer to the range centre (as predicted by Sexton *et al.* 2009). We observed that the recovery of the zero and poor dispersers (0% and 10% dispersal probability) after stabilisation of the temperature took much longer than the changes in genotype distributions under temperature increase. This was the combined effect of several processes. Firstly, the founder events caused a loss of the low dispersive genotypes additional to the loss by selection for the highly dispersive genotype in the newly established populations. This led to decreased persistence of the former genotypes in these populations. As a result, when the climate optimum moved further north, the poor dispersers were not present at a low frequency but had to disperse into these populations from more southern populations. This took a long time due to the second process, which is the very slow movement of the zero and poor dispersing individuals through their incapability of fast dispersal. Thirdly, any dispersal through the establishment and random mating was hampered by swamping with better dispersing individuals present. This slow-down was likely further strengthened by the fourth process, genetic drift, which may cause the loss of an evolutionarily better genotype in small populations.

Perspectives

Our model used a simple representation of the genetic make-up of the dispersal probability. In real life, individual dispersal probabilities may be the result of a wide variety of traits, from adult flight morphology to host selection (for overviews see Hill *et al.* 2011, Ronce 2007). Little is still known of the genetic architecture of most of such traits. Therefore we used a simple genetic model to provide valuable insights into how the demographics of range shifts under climate change could interact with local changes in the frequencies of genotypes. Besides, empirical studies have shown for some species that phenotypic variation for dispersal ability is associated with genetic variation at a single locus, just as we have modelled here (Haag *et al.* 2005, Roff 1986).

We have used climate change scenarios as projected for the coming century to model metapopulation changes in the next 500 years or more. Although this procedure may seem unrealistic in terms of length of time, it proved valuable to have a look into the extreme consequences of a specific change, as the process and the outcome might be similar for e.g. smaller metapopulations or more extreme climate changes, but at a much shorter timescale.

Dispersal probabilities in species have often been found to depend of local habitat quality and population density (Ronce 2007). Many recent studies have incorporated such dependencies to increase

ecological realism in their models (e.g. Cobben *et al.* 2011, Travis *et al.* 2009). In our model the individual dispersal probability is the result of its specific genotype. Therefore dispersal probability could be different for two birds living under the same environmental conditions, which we believe adds further realism to the model (Saastamoinen *et al.* 2009). However, the direct link between the combination of population density and habitat quality, and dispersal probability was lost as a result of this decision. We gained increased interpretability of the results in return. Besides, the selection for a specific dispersal probability occurs through the feedback loop of recruitment and survival, both of which were dependent on habitat quality and population density.

Our study indicates that the founder effect may have significantly contributed to the observed phenomenon of increased frequencies of traits that accelerate range expansion at expanding range margins. We therefore urge researchers in the field to check for this effect and its relative importance (as has been done for some invasive species by Bronnenhuber *et al.* 2011, Roman 2006). If our model results are supported by empirical data this has consequences for the management of natural areas and of protected species under climate change. The good news is that, in the short term, local evolution towards increased frequency of a beneficial genotype may be enhanced by the founder effect (Muenkemueller *et al.* 2011). However, in the longer term this may reduce the genetic diversity and evolutionary potential of species. To ensure that as many potentially beneficial genotypes as possible are present at the expanding range margins, we suggest that increasing the heterogeneity of habitat patches may be an effective management measure (Vos *et al.* (2008) suggested this approach from a demographic point of view). The presence of a wider range of genotypes may enhance the recovery of the original genotype distribution in older populations and after temperature stabilisation as well.

APPENDIX 5.1: DETAILED MODEL DESCRIPTION

For this study we used METAPHOR, a simulation model for metapopulation demography (Verboom *et al.* 2001, Vos *et al.* 2001b). The model has been extended to allow for stochastic temperature zone shifts by Schippers *et al.* (2011). Here a new extension provided each individual in this study with an adaptive diploid gene. The yearly metapopulation demography is simulated based on four events: reproduction, dispersal, survival and aging, in this order. Reproduction and survival are based on population density and habitat quality. Habitat quality is controlled by time and location specific temperature. Dispersal probability depends of the individual's genome. If an individual survives and has offspring, which depends of its location, its DNA will be passed on to the next generation. As such we simulate the effect of stochastic temperature zone shifts on the distributions and carrier numbers of the different genotypes in the metapopulation.

Landscape

The landscape we used in the model had dimensions of 15 km from east to west by 2000 km from north to south. The east and west side were merged to create a cylindric landscape. The landscape contained 3000 circular habitat patches of 50 ha each, so consisted of a total of 5% habitat. When generating the landscape, patches were placed in random positions in the landscape, yet only allowed if they were at a minimum distance of 150 m from existing patches. Five landscape variants with different habitat positions were randomly generated in this way.

Species

We modelled a woodland bird, parameterised as the middle spotted woodpecker (*Dendrocopus medius*). Parameters were based on biological information (Hagemeijer & Blair 1997, Kosenko & Kaigorodova 2001, Kosinski *et al.* 2004, Kosinski & Ksit 2006, Michalek & Winkler 2001, Pasinelli 2000, Pettersson 1985a, Pettersson 1985b) and on the interpretation by Schippers *et al.* (2011) (see Table 5.1). The model distinguishes 2 sexes and 2 lifestages: adults and juveniles. The yearly life cycle consists of recruitment, dispersal, and survival, in this order. Lastly, all juveniles age to adults. Dispersal is dependent of the individual's diploid genome. Alleles may have values of A-F, leading to dispersal probabilities of 0.0-1.0 in steps of 0.1 for the genotypes AA-FF. Recruitment and survival are dependent of life stage, population density (PD) and habitat quality (HQ).

$$PD = N_i / CC,$$

with N_i : number of individuals in patch,

CC : carrying capacity of patch, and

HQ : see section Climate in this appendix.

Species: recruitment function

The number of nests in a patch in each generation is equal to the number of unique adult pairs of opposite sex in this patch, with a maximum of 10. The number of offspring per nest is then found with:

$$N_O = N_{O_PD_0HQ_1} * \left(1 - \left(1 - \frac{N_{O_PD_0HQ_0}}{N_{O_PD_0HQ_1}} \right) * (1 - HQ) \right) * \left(1 - \left(1 - \frac{N_{O_PD_1HQ_1}}{N_{O_PD_0HQ_1}} \right) * PD \right)$$

with $N_{O_PD_0HQ_1}$: number of offspring at population density (PD) = 0 and habitat quality (HQ) = 1, and similar for $N_{O_PD_0HQ_0}$ and $N_{O_PD_1HQ_1}$. See Table 5.1.

Species: survival function

Determines for each individual the chance that it survives the current year, P_S .

$$P_S = P_{S_PD_0HQ_1} * \left(1 - \left(1 - \frac{P_{S_PD_0HQ_0}}{P_{S_PD_0HQ_1}} \right) * HQ \right) * \left(1 - \left(1 - \frac{P_{S_PD_1HQ_1}}{P_{S_PD_0HQ_1}} \right) * (1 - PD) \right) + \sigma_S * N_t$$

with $P_{S_PD_0HQ_1}$: survival rate at population density (PD) = 0 and habitat quality (HQ) = 1, and similar for $P_{S_PD_0HQ_0}$ and $P_{S_PD_1HQ_1}$. See Table 5.1. σ_S is the standard deviation of the average yearly survival and N_t is the yearly random number drawn from a standard normal distribution.

Species: dispersal function

Determines for each individual the yearly chance that it leaves its patch to go on dispersal, P_D .

$$P_D = P_{D_GEN}$$

with P_{D_GEN} being the dispersal probability based on the individual's genome. See Table 5.1.

If an individual disperses, we need to determine where it goes. From their origin patch individuals can go in every direction, along a straight line. Connectivity to other patches is determined by destination patch radius (r) and distance to there (d). So the chance to disperse from patch A to patch B is:

$$P_{AB} = \frac{2 * \arcsin\left(\frac{r_B + l}{d_{AB}}\right)}{2\pi}$$

with l is 150 m, the maximum distance from where an individual can detect suitable habitat. The maximum dispersal distance is 15 km, so habitat patches that are separated by more than this distance are not connected at all. Our model does not allow dispersers to ignore a nearer patch, so more distant patches are located in the shadow of the nearer patch. An individual may arrive in a patch with a population size larger than carrying capacity twice per dispersal event, and is then allowed to disperse again. Should it fail to reach a habitable patch within a total of three dispersal rounds, it dies.

Determines for each individual the yearly chance that it leaves its patch to go on dispersal, P_D .

Climate

Climate is incorporated in the model through habitat quality. Where climate is optimal for the species, habitat quality equals 1, and where climate is unsuitable for the species, habitat quality is 0 (see equation HQ below). Climate change scenarios are based on temperature increase predictions (I °C year⁻¹) by the Hadley Centre of 0.0167 and 0.0333 °C year⁻¹, and we also included a scenario with a temperature increase of 0.084 °C year⁻¹. Besides, the used scenarios include weather variability increase assumptions as temporal stochasticity in the temperature (the current standard deviation of the average temperature σ_t (°C), 0.59 °C) (Schippers *et al.* 2011). Climate in our model is thus defined as the temperature in year t and at location Y . Climate change is then the speed with which temperature isoclines travel north (T km year⁻¹) and the yearly fluctuation of these lines (σ_d km). We use a climatic gradient from south to north of G (°C km⁻¹) to get to:

$$T = I / G, \text{ and}$$

$$\sigma_d = \sigma_t / G$$

This results in a current yearly fluctuation of the temperature isoclines σ_d of 140 km, and we further included scenarios with yearly fluctuations σ_d of 0 km and 280 km. We can then calculate the location of the optimal temperature in north-south direction (Y_{opt}) in a certain year as:

$$Y_{opt,t} = Y_{opt,0} + T * t + \sigma_d * N_t$$

with N_t is the yearly random number drawn from a standard normal distribution.

We obtain a normal habitat quality distribution with this optimal coordinate Y_{opt} in its centre by defining habitat quality (HQ) as

$$HQ_{patch,t} = \exp[-0.695(Y_{opt,t} - Y_{patch})^2 / H^2]$$

H is an indicator of the temperature tolerance of the species, and defined as the distance from the temperature optimum at which habitat quality is 0.5. See Table 5.1.

Initialisation

At initialisation of the model, all habitat patches were filled with 10 adult individuals, equaling half the carrying capacity. Each individual was randomly given 2 alleles, which could have any of the value A, B or C. After initialisation any allele may mutate into any value of A-F at mutation rate of 10^{-6} . The climate optimum Y_{opt} was initialised at 400 km from the southern landscape edge.

Burn-in

After initialisation the model was run for 3000 generations, thus 3000 years. During these 3000 years burn-in, the model runs with temperature isocline speed T equaling 0 in the equation for $Y_{opt,t}$. After this burn-in we started our experiments.

Experiments

In the experiments the temperature isoclines were simulated to move northward for 500 years, under the different scenarios in Table 5.1. Each parameter setting was run twice in each landscape variant (10 runs in total). For studying trends in numbers of individuals we averaged these per parameter setting.

CHAPTER SIX

DISCUSSION

In the previous chapters I have investigated how population demographic processes affect population genetics and how both interact when a species responds to a combination of habitat fragmentation and contemporary climate change. For this I have used one of the most comprehensive eco-evolutionary simulation models in the current literature. This allowed me to explore the genetic compositions of populations across a species range under variable landscape structures at different projections of climate change for different adaptive life history traits. Additionally I assessed the relative importance of founder effects and local adaptation on the resulting genetic compositions. Overall, the main conclusions of the previous chapters are:

1. *The founder effect is an important determinant of the allele composition in newly established populations under range shift across fragmented habitat.*
2. *The genetic impoverishment resulting from such founder events requires considerable restoration time in fragmented habitat and consequently it is a risk to species' survival.*

The results of this thesis are scientifically relevant as the interaction of population demography, population genetics and habitat structure under projections of contemporary climate change have thus far been relatively little investigated. The results and their interpretation increase the understanding about metapopulation genetics under climate change. They indicate that founder events may have a profound and long-lasting impact on the genetic structure across species ranges. This result contributes to the interpretation of data collected in the field and provides insight into the possible causes of observed genetic patterns. Therefore, this thesis may contribute to the improved design of field studies and the data analysis for both scientific and management purposes. Furthermore, the results of this research offer insights for the conservation of species and their genetic diversity in fragmented landscapes under climate change.

Reflection

The genetic variation in a recently established population consists of the combined genetic variation of the founding individuals. If the genetic variation in these individuals is only a subset of the variation present in their origin population or populations, due to the sampling error resulting from the small number of founders, the new population is genetically different from the ancestral populations. This is called a founder event, and the chance of its occurrence increases with the increased level of fragmentation of a species' habitat. A network of small interconnected habitat patches implies frequent population extinctions and recolonisations of patches by a limited number of individuals. A founder event mostly comprises a reduction of genetic variation in the recently established population (Lee 2002, Mayr 1942).

The change in genetic composition from the ancestral to the newly established population implies a change in allele frequencies. Not otherwise affected by selection, the frequencies of neutral alleles provide the most straightforward observations of the founder effect. Many studies have described a reduction in neutral genetic diversity caused by founder effects in species expanding their range under temperature increase, both contemporary and after the last glacial maximum (Balint *et al.* 2011, Excoffier *et al.* 2009, Garroway *et al.* 2011, Hewitt 1996, Hill *et al.* 2011). Founder effects may also affect the frequencies of adaptive alleles in new populations. This may enhance or impede the survival of the

established population, depending on the selective value of the random alleles increased in frequency. Many studies on mutations associated with human diseases have related founder effects to the establishment of these mutations (Brauch *et al.* 1995, Reitsma *et al.* 1991, Telatar *et al.* 1998, Weitzel *et al.* 2005). Travis *et al.* (2007) show in a simulation study that founder effects may cause the establishment and frequency increase of deleterious mutations in species under range shift. Founder events may also cause the frequency increase of beneficial alleles (Muenkemueller *et al.* (2011), this thesis), where the increase is further supported by local selection for these alleles after establishment. In such cases, when founder event and selection both lead to increased frequencies of alleles, it is hard to separate the respective impacts of founder effects and local adaptation on the evolutionary process in the new population.

The founder effect was introduced by Mayr (1942) as the ‘founder principle’. In his view it was one of the mechanisms causing the reduced genetic diversity in populations, which could promote rapid evolution and cause speciation (Provine 2004). Some empirical studies have confirmed this by suggesting a causal relationship between a reduction of genetic diversity and local adaptation (Kliber & Eckert 2005, Tsutsui *et al.* 2000). Regarding the combination of founder effects and rapid evolution, Reznick and Ghalambor (2001) show in a review of empirical studies that contemporary adaptation generally occurs either upon colonisation of new environments, or in the context of metapopulation structure and heterogeneous environments. In recent years many empirical studies have shown local evolution at the margins of species ranges expanding under climate change, see review of Hill *et al.* (2011). In this thesis I show that founder effects pronouncedly enhance the local adaptation of the newly established populations during the range shift of a woodland bird with moderate dispersal capacity in fragmented habitat. This is caused by a reduction of genetic diversity that favoured the locally best-adapted genotype, because founding individuals are not a random sampling of the ancestral populations, particularly when dispersal capacity is concerned (Provine 2004). The allele with the highest frequency in the ancestral population, or the individuals with the highest dispersal capacity have the largest chance to found the new populations. The occurrence of founder events may therefore be regarded as positive as it may increase the rate of local adaptation and thus the increased short-term survival of species under range shift. However, the model results also indicated that the reduced genetic diversity upon founder events impeded local adaptation in these populations at a later stage, when balancing selection was to be expected in locations closer towards the species’ range centre. So founder events may in this later stage impede the survival of these populations. This finding indicates that it is of great importance to assess the relative contribution of founder effects in evolutionary processes in populations established beyond the original range limit under range shift, especially in fragmented habitat. While founder effects have been clearly associated with the patterns in neutral genetic diversity observed after range expansions (Garroway *et al.* 2011, Hewitt 1996, Hill *et al.* 2011), studies showing trait evolution under range shifts have thus far not investigated the potential role of founder effects.

It has been suggested that range shifts and local adaptation as species’ responses to contemporary climate change can complement each other to increase species survival (Hoffmann & Sgro 2011, Parmesan 2006). Hill *et al.* (2011) suggested that there is a positive feedback between range expansion and the evolution of traits that accelerate such expansion. The results in this thesis imply that in

fragmented habitat range shifts are prone to cause founder events. These may enhance local adaptation at the expansion front of the range in first instance but impede adaptation when selection pressure changes at a later stage. Positive feedback may thus indeed be observed, possibly even to a larger extent than expected through the enhancement by the founder effect. I wish to stress that the positive aspects of founder events may be temporary and their long-term adverse effects should be quantified and taken into consideration.

METHODOLOGICAL CONSTRAINTS

In this thesis I investigated how population demographic processes affect population genetics and how both interact in a species responding to contemporary climate change in fragmented habitat. For this I used a simulation model. Simulated data are the outcome of the interaction of the model assumptions, and the observed patterns and trends only reveal processes that were allowed to take place in the simulation model. This underlines the importance of the quality of the model assumptions and the incorporated processes. The model I used throughout this thesis is an individual-based, stochastic, spatially explicit eco-evolutionary model. This has several implications. It means that it includes many processes that are considered important when investigating population demography and genetics in a species' range under climate change-induced range shifts in fragmented habitat. However, it also implies that the outcome is the result of a complex system of processes, impeding the interpretability of the data.

I used a single simulation model to study four different research questions. The model was sufficiently comprehensive to investigate all four questions, which implies that it may be an efficient strategy to invest in the design, development and verification of a model that is suitable to address a wider range of scientific challenges. This approach is fairly uncommon in the ecological modelling community, which mostly develops models from scratch to answer single questions. Such an efficient strategy however also has several drawbacks, most importantly the risk of model over-complexity. The inclusion of many model parameters leads to an exponential increase of the number of process interactions in the model. As a consequence the specific eventual effect of the single model parameters on the model results may be hard to deduce, with the risk that the model becomes a 'black box'. In that case, the model ceases to improve the understanding of the modelled system. Such models are for example used for realistic projections of global temperature increase by the year 2100, and require a careful calibration with empirical data. The assessment of all parameter effects under all combinations of parameters and model scenarios prevents model over-complexity. This is an elegant approach and common practice for more theoretical models, designed to maximise the understanding of a (single) process. Due to their simplified assumptions there is however an increased chance that the *outcome* of such models will never be encountered in the field. A good example is the outcome in this thesis that the investigated metapopulation decreases in size upon higher rates of temperature increase, regularly leading to the observed extinction of the species in time. These observations were the result of the modelled processes and the combination of the projected global temperature increase, the investigated landscape structure and the realistic estimates of life history parameter values. When using a theoretical

model the parameter combination leading to the extinction of the species would have been omitted for lack of relevance to these specific research questions. I am afraid that the current rate of knowledge development will not keep pace with the increased demand for information to deal with the very complex environmental issues caused by habitat fragmentation and climate change if we limit ourselves to such theoretical models. A second drawback of the use of a single model to answer four different scientific questions is the interdependence of the model results. It requires thorough model verification to preclude that the four chapters of this thesis observe a strong effect of founder events in species under range shift, all based on the same modelling error.

Here I will further elaborate on the restrictions of my main conclusions as a result of the model assumptions. Hill *et al.* (2011) stated that '[v]ariation [in level of reduction of genetic variation under range shift] among species is likely to reflect different patterns of dispersal and habitat availability, coupled with differences in life-history traits (e.g., affecting population growth) and different numbers and locations of refugial populations.' I have used a single species and its life history parameters as input for the calculations made in this thesis. The use of a detailed life history in the model has increased its level of realism and thus improved its applicability to the interpretation of empirical data subjected to the interaction of population genetics and demography in species in fragmented habitat responding to climate change. Besides, the model species *Dendrocopus medius* was chosen for its average dispersal capability and moderate population growth rate, thus increasing its usefulness as a model species by not occupying either end of these parameter spectra. However, I have not assessed how the specific species' life history parameters affected the results in this thesis, thus generalisation of the results across a wider range of species and eco-profiles should be done with care. For example, mitigation of the loss of neutral genetic diversity under range expansion can occur through a dual dispersal strategy (Bronnenhuber *et al.* 2011) or multiple establishments (Roman 2006). Hill *et al.*'s (2011) statement further included the effect of the level of habitat availability. In Chapter 3 I have made an assessment of the effects of varying the number and the sizes of habitat patches on the level and distribution of neutral genetic diversity throughout the species' range in response to different rates of climate change. The effects caused by founder events were present across this array of habitat structure. However, effects of increased spatial heterogeneity and the presence of mountain ranges or other dispersal barriers have not been investigated in this thesis. These effects are likely to be substantial and thus the extrapolation of the results to species' ranges across increased heterogeneous habitat should be done with caution.

In this thesis I have used global temperature increase projections by the Hadley Centre from a report from the year 2003. The rate of development and accuracy of such projections has been greatly increased in the last years, and recent empirical data have shown that global temperature has kept track of the largest of these predicted increases. However, local, regional and national projections of changes in temperature and weather variability can show considerable differences from the projections made for the global averages. To deal with such uncertainty I included, in each of the proceeding chapters, three different levels of global temperature increase and a wide range of the stochastic variation of the yearly temperature. Under all climate change scenarios the results showed similar trends, with predictable differences, and the same is true for the effects of temperature stochasticity.

The genetic architecture of the neutral genetic variation as modelled in this thesis can be deemed fairly sophisticated when compared to modelling efforts in other, more theoretical studies (Arenas *et al.* 2011, McInerny *et al.* 2009, Travis *et al.* 2007), as I for example used diploid inheritance. However, the traits subjected to adaptation as studied in Chapters 4 and 5 have been modelled in a more simplified matter. The reasons for this simplification are clear. The extent to which a trait has a genetic component is unknown for many life history traits of many species, especially regarding complex traits such as the ones used in this thesis. In addition, the genetic architecture of life history traits has hardly been investigated for species others than humans and commercially used breeds and varieties. I have therefore opted for the more theoretical approach and maintained the genetic model of the traits as simple as possible to improve the interpretability of the results. However, increased complexity of such traits may affect the results as observed in this study. Quantitative traits will for example show a wider range of phenotypes and the resulting gradient of selected offspring is likely to reduce the levels of maladaptation as observed, particularly, in Chapter 4. The interaction of local adaptation and founder effects on a combination of different life history traits is a further interesting improvement with a likely effect on the model outcome.

SUGGESTIONS FOR FURTHER RESEARCH

I propose that further research is conducted in two complementary directions. First, research aimed at explaining complex eco-evolutionary dynamics under habitat fragmentation and climate change, through both model and empirical experiments. Second, research to find successful strategies for the conservation of genetic diversity under habitat fragmentation and climate change.

Model studies

I propose the further development of realistic, species-specific eco-evolutionary models to increase both understanding and predictive power of the interaction of demographic and genetic responses of species to combined pressures of habitat fragmentation and climate change. Hoffmann and Sgrò (2011) also mention such realistic, predictive models in their future directions. Such models will contribute to the disentanglement of genetic signatures of demographic processes such as spatial expansions and retractions, from signatures of selection and adaptation, which is deemed important by Excoffier *et al.* (2009) as well. To increase the usefulness of such models and their credibility, to divide the development and verification effort and to prevent scientific monopolies, the development of such models should be conducted in an open-source community and their use open to all. The explicit modelling of the genetic architecture of important life history traits should be prioritised. In addition, the interaction of different species, different life history traits and of genetic and phenological traits deserve attention in modelling studies. Finally, although the large research effort for the processes at the expanding range margin has greatly advanced our understanding, it should now be offset by assessments of processes across species ranges and at retracting range margins, as indicated by Hampe and Petit (2005), Hill *et al.* (2011), Hampe and Jump (2011), and taken up by Arenas *et al.* (2011), McInerny *et al.* (2009) and in this thesis.

Empirical studies

The results of this thesis indicate that founder effects may play an important role in the observed rapid evolution of traits in populations established beyond the original range limit under range shifts, possibly affecting the adaptive potential of these populations when the selection pressure changes. These findings may contribute to the interpretation of empirical data revealing evolutionary processes upon range expansion. Additionally, they imply that it is of great importance to assess whether such founder events have contributed to the observed trait evolution. Nolte (2011) underlines the importance of such assessments with regard to invasive species. In this thesis I have combined the study of changes in adaptive traits with the assessment of signatures of founder effects in neutral markers, both in the same individuals. I advocate that field studies investigating the evolution of life history traits under conditions in which founder events are to be expected, such as range expansions and in metapopulation structures, are designed in similar manner. Such empirical studies can then detect whether any observed evolutionary process is accompanied by a signature of founder events under range expansion, indicating the likeliness that local adaptation was enhanced by founder effects.

Additional empirical studies to assess which life history traits are of importance for the survival of species in fragmented habitat in response to contemporary climate change, and to get an indication of their genetic architecture, are of great importance to increase our understanding and eventually advance predictive modelling power.

Conservation strategies

International biodiversity conservation strategies have been aimed at reaching or maintaining robust population sizes of threatened species by enlarging and connecting natural areas and increasing habitat quality (for example the European Natura 2000 conservation network). In response to climate change many studies have proposed additional conservation efforts of the same nature, to increase the permeability of the landscape for range shifting species and to improve species resilience (Galatowitsch *et al.* 2009, Poiani *et al.* 2011, Vos *et al.* 2008). However, the conservation of genetic diversity has hardly been a consideration in both current and proposed conservation strategies (Laikre *et al.* 2010). The conservation of genetic variation has mostly taken place *ex situ* in gene banks and mainly for species of commercial interest (Laikre *et al.* 2010). Many empirical and modelling studies however indicate that even species that are (predicted to remain) demographically unaffected by (certain rates of) climate change, can be exposed to genetic changes, either evolutionary or in neutral genetic variation (Excoffier *et al.* 2009, Hill *et al.* 2011, Thomas *et al.* 2001, Travis *et al.* 2007). These changes may result in loss of genetic biodiversity and loss of evolutionary potential, leading to maladaptation and decreased species resilience to climate change. It is therefore important to investigate potential strategies for the conservation of genetic diversity. This should be aimed at assessing to what extent current conservation efforts by means of increasing habitat quality and stabilising networks are of use. Hampe and Jump (2011) mention the conservation of populations at retracting range margins, that can persist in enclaves of good environmental conditions within an otherwise inhospitable region, and that, as shown in this thesis, may maintain unique genetic variation lost elsewhere. If necessary, additional strategies should be identified by modelling studies and consecutive field experiments. For example, the ecological

implications of the translocation of species (Galatowitsch *et al.* 2009) and genetic material (Smulders *et al.* 2009) requires attention for species that are identified to have little or no other possibilities.

IMPLICATIONS FOR POLICY

Policymakers are responsible for translating the needs of society into policy leading to the satisfaction of those needs. For this, policymakers need scientific input to get an overview of all possible policies and to assess if a certain policy has the desired outcome. Should society feel that nature conservation is important and in majority agree that this is a worthy expenditure of public funds, then policymakers may request researchers to propose measures which would counteract the threats to the survival of biodiversity. This thesis was part of such a request. The government in The Netherlands asked how the climate as experienced in The Netherlands would change in the future, how this would affect society and how spatial design could support adaptation to and mitigation of climate change (www.klimaatvoorruijnt.nl).

From this thesis I deduce the following conclusions with relevance to the conservation of species confined to fragmented landscapes and subjected to climate change, and their genetic diversity.

1. When a species colonises habitat sites in a newly available climate zone the local populations are likely to be genetically impoverished compared to the populations in the original part of the range, that have existed for a long time period. This loss diminishes the long-term adaptive potential of these populations.
2. Therefore, the original source populations of a species under range shift, specifically those in the original range centre, contain the most of its overall genetic variation.
3. The conservation of this genetic variation can be enhanced by increasing habitat area and decreasing the rate of climate change.

From these conclusions I deduce that the survival of a species under climate change crucially depends on the possibility to shift its range in concurrence with its preferred climate conditions. Its chance of success may be enlarged by slowing down the rate of climate change and by creating a permeable landscape structure. During such a range shift only a subset of the overall present genetic variation will reach the newly colonised region. New populations will therefore be genetically different from original populations and these differences may exist for many decades. The species' genetic diversity is thus mostly present in the original populations. So the persistence of this genetic diversity largely depends on the survival of these original populations throughout the period of climate change. A suitable landscape structure, which enlarges habitat patches and connects isolated habitat patches and networks, local management to optimise habitat quality, and a decrease of the rate of climate change may all enhance the persistence of these original populations, and thus of their present genetic diversity.

The urgency with which described measures should be taken in order to conserve genetic biodiversity is dependent of the size of a specific species' range and the rate of temperature increase. In this thesis the extinction of the model species was observed after 150 to 200 years for the temperature increase scenario of 4 degrees Celsius increase by the year 2100, while the initial range size was approximately 1000 kilometres of fragmented habitat but without major dispersal barriers. The middle

spotted woodpecker is an average disperser with average population growth rate, and many species ranges are intersected with dispersal barriers such as urbanised areas and mountain ranges. This implies that a substantial number of species may face extinction within 150 years. In addition, the changes in genetic structure due to range shifts and the accompanying founder events in fragmented habitat take effect immediately, with loss of species-specific genetic variation upon range retraction. Thus, if the conservation of genetic variation is desired, this further increases the urgency with which species are to be assessed and appropriate measures taken, especially when taking into account that the creation of a suitable landscape structure may take twenty to one hundred years, dependent of the required environmental conditions.

SAMENVATTING

INTRODUCTIE

Onze planeet wordt bewoond door 7 miljard mensen, die samen substantiële hoeveelheden ruimte en natuurlijke hulpbronnen gebruiken. De omvorming van natuurlijke gebieden naar steden, landbouwgronden, wegen en industriële gebieden hebben grote veranderingen teweeg gebracht in het landschap, maar ook in de atmosfeer, waterlichamen en de bodem. Door deze veranderingen worden veel natuurlijke soorten bedreigd, soorten die van belang zijn voor de (toekomstige) overleving van de mens. Twee belangrijke huidige bedreigingen voor biodiversiteit zijn het verlies en de verslechtering van het natuurlijke habitat en klimaatverandering. Terwijl de effecten van ieder van deze factoren op biodiversiteitsverlies intensief worden onderzocht, weten we nog steeds erg weinig van de complexe interacties tussen habitatverlies en klimaatverandering en de reacties van wilde soorten hierop.

In reactie op klimaatverandering verschuift van veel soorten het areaal, maar het is duidelijk dat dit voor lang niet alle soorten snel genoeg gaat. Habitatfragmentatie zal in het algemeen de noodzakelijke areaalverschuivingen vertragen. Er is geopperd dat de combinatie van areaalverschuivingen en de lokale aanpassing van soorten aan de veranderende omstandigheden hun overleving positief zal beïnvloeden. Habitatfragmentatie heeft in theorie meerdere effecten op het aanpassingsvermogen van soorten. 1. Kleinere populaties bevatten minder genetische variatie. De toename van de frequentie van een gunstig genotype ten koste van de andere verloopt daarom sneller in kleine populaties. Maar 2. de invloed van toevalsprocessen als genetic drift en founder effects is groter in kleine populaties. In dat geval neemt niet de frequentie van een gunstig genotype toe in de populatie maar van een willekeurig ander genotype. De populatie raakt dan niet beter aangepast aan de nieuwe omstandigheden. Als we willen weten hoe de combinatie van zo'n gunstig en ongunstig effect uiteindelijk de overleving van een populatie beïnvloedt is het dus noodzakelijk om alle processen te kwantificeren. Vooral het aandeel van founder effecten in het evolutieproces is nog weinig onderzocht. Bij een founder effect heeft de populatie in een net gekoloniseerde habitatplek een andere genetische samenstelling dan de bronpopulatie van de koloniserende individuen. Dit komt doordat deze individuen geen correcte afspiegeling zijn van de bronpopulatie. In dit proefschrift heb ik een ruimtelijk expliciet, individu-gebaseerd eco-evolutionair model gebruikt om de interactie van het founder effect en lokale adaptatie te onderzoeken in gefragmenteerde populaties van middelste bonte specht gedurende klimaatverandering.

VRAGEN EN ANTWOORDEN

Het gevolg van opeenvolgende founder effecten gedurende de uitbreiding van een soortareaal is dat de genetische variatie in de nieuw gekoloniseerde gebieden lager is dan in het oorspronkelijke verspreidingsgebied van de soort. Zo een verlaagde genetische variatie in nieuwe gebieden is voor veel soorten aangetoond in het veld. Er was echter nog niet onderzocht wat voor een consequenties dit op termijn heeft voor het gehele verspreidingsgebied van een soort bij de voorspelde temperatuurstijgingen. In *hoofdstuk 2* beantwoord ik daarom de vraag: *Wat voor een effect heeft de verschuiving van een soortareaal op de hoeveelheid en de verspreiding van neutrale genetische variatie voor het gehele verspreidingsgebied van een soort in gefragmenteerd habitat onder voorspelde temperatuurstijgingen?* In dit hoofdstuk laat ik zien dat

opeenvolgende founder effecten voorkwamen onder alle voorspelde temperatuurstijgingen. Op termijn betekende dit een afname van neutrale genetische variatie in het gehele verspreidingsgebied, onafhankelijk van het verlies aan aantal individuen van de soort. Deze resultaten geven aan dat de huidige indicatoren die worden gebruikt voor het monitoren van biodiversiteit en gebaseerd zijn op het voorkomen en de aantallen individuen van soorten geen goede weergave zijn van wat er gebeurt met de genetische variatie van een soort. Daarnaast geven ze het belang aan van het behoud van gebieden waar soorten een langere tijd hebben geleefd omdat zich daar de meeste genetische variatie bevindt.

Voor wilde soorten is er nog nauwelijks aandacht geweest voor de monitoring van genetische variatie en beheerplannen voor het *in situ* behoud van deze variatie. Versterking van het habitatnetwerk door het vergroten van habitatplekken en hun verbondenheid zorgt aantoonbaar voor grotere en levensvatbaardere populatienetwerken. In *hoofdstuk 3* stel ik dus de vraag: *Heeft landschapsstructuur een effect op het overleven van neutrale genetische variatie onder areaalverschuiving?* De resultaten van dit hoofdstuk laten zien dat een toename van het habitatareaal in een landschap het behoud van de genetische variatie verlengde. Deze areaaltoename verhinderde echter niet dat nieuwe populaties minder genetische variatie hadden dan de oorspronkelijke populaties als gevolg van founder effecten. Ik concludeer daarom dat toegenomen verbondenheid van populaties binnen het habitatnetwerk het verlies aan genetische variatie vertraagt, maar dat extra maatregelen nodig zijn om dit verlies op termijn te voorkomen. Een ander belangrijk resultaat is dat een goed verbonden landschap onder stabiele omstandigheden niet per se optimaal verbonden is onder klimaatverandering. Voor beheerders die een strategie willen ontwerpen om genetische variatie *in situ* te behouden is dit belangrijke informatie.

Veel soortverspreidingsgebieden laten genetische verschillen zien tussen populaties die in het centrale deel van het gebied liggen en populaties die in de gebiedsmarges voorkomen. In *hoofdstuk 4* beantwoord ik de vraag: *Wat zijn de consequenties van de interactie van lokale adaptatie en founder effecten onder de verschuiving van een soortareaal waarbinnen genetische verschillen bestaan tussen centrale en marginale populaties?* In dit hoofdstuk heb ik mijn modelsoort een gen gegeven dat bepaalde in welke mate een individu was aangepast aan een optimale temperatuur. Generalisten hadden een grote temperatuurtolerantie, maar een algemeen lage fitness (dus kleinere overlevingskansen en minder nakomelingen). Specialisten hadden een hoge fitness, maar een lage temperatuurtolerantie. Onder stabiele omstandigheden hadden specialisten het selectievoordeel in het centrale deel van het verspreidingsgebied, rond het temperatuuroptimum. De generalisten bewoonden dan de marginale delen, waar ze beter aangepast waren dan de specialisten. Onder temperatuurstijging breidden de generalisten zich uit naar de gebieden die nieuw beschikbaar kwamen. Gecombineerd met areaalverschuiving leidde dit ertoe dat de generalisten op termijn ook het centrum van het areaal bewoonden, terwijl de specialisten werden teruggedrongen naar de terugtrekkende areaalgrens. Dit was het gevolg van founder effecten en resulteerde in een slechte aanpassing van de soort met negatieve gevolgen voor de grootte van de metapopulatie en het soortvoortbestaan.

Voor een aantal soorten hebben onderzoekers aangetoond dat er evolutie van dispersiecapaciteit heeft plaatsgevonden in nieuwe populaties onder areaaluitbreiding. In *hoofdstuk 5* vraag ik: *Kan toegenomen dispersie in populaties aan de uitbreidende grens van het areaal het gevolg zijn van founder effecten?* In dit hoofdstuk laat ik zien dat de hoge frequentie van individuen met een grote dispersiekans in nieuwe populaties het

gevolg was van de combinatie van lokale adaptatie en founder effecten. Doordat goede disperseerders het selectievoordeel hadden in de buurt van de areaalgrenzen waren ze daar in grotere aantallen aanwezig dan de minder goede disperseerders. Gecombineerd met de hoge dispersiekans hadden ze dus de grootste kans om nieuwe populaties te stichten. Hoewel ze in deze nieuwe populaties ook het selectievoordeel hadden waren hun frequenties verhoogd tot boven wat evolutionair wenselijk was als gevolg van het founder effect. Dit leidde bij veranderende selectiedruk tot afgenomen adaptatievermogen.

DISCUSSIE

In hoofdstuk 6 reflecteer ik op de resultaten van de voorafgaande hoofdstukken. De belangrijkste algemene conclusies zijn:

1. Founder effecten bepalen in belangrijke mate de genetische compositie van nieuwe populaties onder areaalverschuivingen die zijn veroorzaakt door klimaatverandering.
2. De periode tot herstel van de hoeveelheid genetische variatie in deze populaties is aanzienlijk met een negatief effect op de overleving van de soort als gevolg.

Er is geopperd dat de combinatie van areaalverschuivingen en de lokale aanpassing van soorten aan de veranderende omstandigheden hun overleving positief zal beïnvloeden. In een andere overzichtsstudie wordt gesuggereerd dat er een positieve terugkoppeling bestaat tussen areaaluitbreidingen en de evolutie van eigenschappen die zo een uitbreiding versnellen. De resultaten van dit proefschrift impliceren dat areaalverschuivingen in gefragmenteerde landschappen founder effecten veroorzaken. Deze kunnen lokale adaptatie initieel bespoedigen, maar voorkomen de aanpassing van de populatie in een later stadium, als de selectiedruk verandert. Ik kan dus bevestigen dat er een positieve terugkoppeling is tussen areaaluitbreidingen en de evolutie van eigenschappen die hiervoor gunstig zijn. Deze terugkoppeling is misschien wel sterker dan gedacht, doordat founder effecten hier een rol in spelen. Hier wil ik benadrukken dat deze positieve aspecten van founder effecten tijdelijk kunnen zijn en dat hun lange-termijn negatieve gevolgen moeten worden gekwantificeerd en meegenomen in zowel onderzoek als beheerplannen.

Beperkingen van de methode

Voor het onderzoek beschreven in dit proefschrift heb ik een simulatiemodel gebruikt. De geobserveerde patronen en ontwikkelingen in de gesimuleerde data bestaan dus alleen uit processen die in het model zijn meegenomen. De kwaliteit van de modelprocessen en -aannamen zijn daarom van groot belang. Het model dat ik heb gebruikt is een individu-gebaseerd, stochastisch, ruimtelijk-expliciet eco-evolutionair model. Dit betekent dat het model veel processen bevat die belangrijk worden geacht voor populatiedemografie en -genetica bij het schuiven van arealen onder klimaatverandering in gefragmenteerde landschappen. Het nadeel hiervan is dat de resultaten het gevolg zijn van de interactie van veel processen en dit belemmert de interpretatie van de resultaten.

Suggesties voor toekomstig onderzoek

Het gebruik van modellen kan veel inzicht verschaffen in de oorzaak van bepaalde waarnemingen in het veld. Hiermee kunnen we richting geven aan veldexperimenten. Op basis van het onderzoek in dit proefschrift doe ik voorstellen voor toekomstig onderzoek in twee, elkaar aanvullende, richtingen.

1. Verder onderzoek naar complexe eco-evolutionaire dynamiek in gefragmenteerde landschappen onder klimaatverandering, zowel met model- als empirische experimenten. Voor modelstudies stel ik de ontwikkeling voor van meer gedetailleerde modellen zoals het hier gebruikte. Het is mijn overtuiging dat complexere modellen belangrijke patronen weergeven die anders niet worden waargenomen. Zulke modellen moeten bij voorkeur gezamenlijk worden ontwikkeld en gebruikt in combinatie met strategische modellen. Voor veld- en labonderzoek stel ik voor om experimenten te ontwikkelen die kunnen testen of eerdere geobserveerde snelle lokale adaptatie in het veld veroorzaakt kan zijn door founder effecten. Dit is belangrijk omdat dit nadelige gevolgen kan hebben voor het adaptatievermogen van dergelijke populaties in een later stadium. Daarnaast stel ik voor om 2. te onderzoeken in hoeverre huidige maatregelen om biodiversiteit te behouden, zoals het vergroten en verbinden van natuurlijke gebieden, ook geschikt zijn voor het behoud van genetische variatie. Uit mijn en eerder onderzoek blijkt dat juist populaties die aan de terugtrekkende grens van het soortareaal liggen veel unieke genetische variatie kunnen bevatten. Het is van belang te onderzoeken met welke beheermaatregelen we deze populaties zo lang mogelijk kunnen behouden. Voor soorten die weinig of geen andere mogelijkheden hebben moet worden uitgezocht wat de voor- en nadelen zijn van translocatie naar gebieden die voorlopig een geschikt klimaat houden.

Implicaties voor beheer

Uit dit proefschrift trek ik de volgende conclusies met betrekking tot het beheer van natuurgebieden:

1. De populaties in natuurlijke gebieden die recentelijk zijn gekoloniseerd door een soort zijn genetisch verarmd ten opzichte van de bronpopulaties van deze soort. In deze periode zijn de nieuwe populaties potentieel kwetsbaar door verminderd aanpassingsvermogen.
2. De bronpopulaties van een soort, met name die in het oorspronkelijke centrum van het areaal, bevatten relatief veel en unieke genetische variatie.
3. Het behoud van deze genetische variatie is gebaat bij een groter areaal aan natuurlijke gebieden en een afname van de temperatuurstijging onder klimaatverandering.

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DANKWOORD

Background

It does not seem that long ago, the phone call. But when I come to think of it, it actually is. Life was different back then. More simple in some ways, more complicated in others. Just different, I guess. For starters, we were living in Norway. And we liked it. The landscape, the quietness, the people. Not the weather, no. But the light. And the outdoor life. Skiing and barbecuing, who would think of that combination but a Norwegian. Barbecuing on the beach. A lot of barbecuing apparently, maybe that is what it was. Sea kayaking and ice skating. I have not met a representative of any nationality who was more into sports than the Norwegians. (Well, maybe Daniela...) Drive for three hours, put your skis on your back and hike up the mountain for another three hours, put your skis on and find yourself next to your car again half an hour later, to drive back home for yet another three hours. What kind of person does something like that? A Norwegian. Fantastic country to raise children too. You get a year off work when they are born. Then they go to day-care, and you can find them walking in pairs, holding hands, in the forest to pick blueberries in their safety vests. So cute. At least until they reach the age of ten, when they inevitably start drinking, a lot, the second national sport after cross-country skiing. We liked this country so much that we decided that we would stay after Ingo's PhD graduation. Him getting a job would not be a problem at all. And me, I was fine. For years I had not had a job that I really liked, since my MSc graduation. So this freelance researcher thing with John at NINA was actually quite nice. My CV was getting better in any case. The people were lovely. I was making some money. So I was fine. I was going to find a nice PhD-project soon enough. And I knew exactly what I wanted too. Something with population genetics. Or climate change. Maybe both, that would be great.

In ten years' time Ingo may leave you for his secretary, and then you'll regret it. It made me laugh, the very thought of Ingo having a secretary. But it did open a little window in my head. *You can always move back here after your graduation.* That one kicked the door wide open and I had made up my mind. We were moving back to the flat country.

So here we are, five years later. An era later. A house in Noordwest, two children and a family car, holidays in Landal Greenparcs, chicken pocks and chalk powder. No more sunny afternoon coffees at the Café Filter, no more membership of the club of international students. But life is good. The sky is wide and the wind is hard. There is giggling at the back of the bike. And at the front. The barbecue is still hot, but we don't have to warm our hands at it. And the thesis...? The thesis is finished.

Jana, dat telefoontje kwam van jou. Dankjewel. Robert and John, thanks for your advice. I am glad I took it. There is no secretary in sight thus far by the way. And we are not moving back to Norway.

Het proefschrift

Paul en Rolf, dank voor jullie vertrouwen, advies en eerlijkheid. Jullie waren altijd bereid tot constructief meedenken en zo nodig bijsturen. Vooral in de afrondende fase hebben de vele discussies en snelle commentaren het wordingsproces flink gestroomlijnd.

Jana, ik geloof dat ik in mijn leven van niemand meer en mooiere complimenten heb gekregen dan van jou (en let wel: ik tel Ingo hier gewoon mee). Al twaalf jaar geef jij me het gevoel dat ik alles kan. Je directe inmenging in dit werk heeft zich in de laatste maanden beperkt tot je specifieke expertise

(en die is zeker niet gering), maar indirect ben je overal bij betrokken. Dankzij jou heb ik deze positie gekregen. Je stelt me voor aan de mensen die ik moet kennen. Je ziet kansen die anderen niet zien. En je rust, warmte en vertrouwen hebben een belangrijke bijdrage geleverd aan mijn zelfvertrouwen. Het zelfvertrouwen dat ik zo lang niet heb gehad en dat zo nuttig blijkt. Dankjewel.

En dan René. Van het aantal keren dat ik je achter het behang heb willen plakken ben ik de tel kwijt geraakt. Maar ik ga ervan uit dat de wederzijdse gevoelens een zelfde ordegrootte bereikt hebben. Ik ben blij te constateren dat dit allemaal jaren geleden is. En inmiddels kan ik met gerust hart beweren dat ik iedere promovendus zo'n begeleider gun als jij. Nu kan ik met gemak pagina's uitweiden over je niet aflatende enthousiasme, je soms bijna betreurenswaardige optimisme, je schier oneindige vakkennis, je constante stroom aan nieuwe ideeën, je oeverloze leergierigheid, je nou ja, *pagina's* dus. Maar waar ik me werkelijk over verwonder is het schijnbare gemak waarmee je, te pas en te onpas, uren, en dan bedoel ik letterlijk *uren*, tijd vrij maakt in wat toch een vrij vol schema moet zijn, om mij, meestal stante pede, te helpen met een nuttige discussie. Tot zover *verwondering*. Waar ik je vooral om *bewonder* is een eigenschap waar ik bijzonder veel plezier aan heb beleefd: het concentratievermogen dat je kunt opbrengen om onder heel veel omstandigheden aan vier volledig uit hun context gerukte woorden van mij voldoende te hebben om 1) je weer te herinneren wat het specifieke probleem was, en 2) de laatste stand van zaken met betrekking tot de oplossing van dit probleem, en daarnaast 3) ook nog met een nuttig antwoord te komen, bij herhaling binnen twee minuten, via mobiele telefoon, in een overvolle trein. Alleen een beetje jammer dat je verwacht dat ik die eigenschap ook heb... Dankjewel René, voor al je kennis, al je enthousiasme, al je tijd.

En tot slot in dit rijtje van onmisbare proefschriftbouwers: René 2 alias René Jochem alias René J. Zelden heb ik iemand ontmoet met zo'n grote 'ik heb er zin an'-uitstraling. Je enthousiasme en levensvreugde werken bijzonder aanstekelijk. Je 'doe-maar-normaal-dan-doe-je-gek-genoeg'-instelling heeft me toch met enige regelmaat behoed voor aan wanhoop grenzende mismoedigheid. Heel fijn bovendien dat je 23 keer dezelfde vraag hebt willen beantwoorden (in ieder geval heb ik het je niet moeilijk gemaakt). En tot slot dank voor *het creatieve tijdschrijven*, redder in de (financiële) nood.

De werkomgeving

And now off to my much-valued circle of colleagues. I would like to thank here professor Bernt-Erik Sæther for providing me with a fully facilitated Trøndersk workspace in the first year of this PhD-study, including a lovely, international group of intelligent, ambitious, yet warm and friendly PhD-students and postdocs.

Na onze verhuizing naar Nederland heb ik mijn intrek genomen in een heerlijk kantoor met veel licht en uitzicht. De samenstelling van ons kippenhok is in de loop der jaren veranderd van 'Nederlands + vrouw', met een licht exotisch tintje in de vorm van Adriana en Brigitte, naar een 'gemengd + gemengd' gezelschap. I would like to thank the many office mates who have kept me company throughout the years on the road towards this thesis. I greatly value the many, *many* conversations on a large, *huge* variety of subjects, ranging from climate-controlled bedrooms to politics, from recipes to supervisor management, from holiday plans to contemplations about future careers or lack thereof. All the best to all of you (and see you at lunch next week).

My working environment at PRI/Plant Breeding was (fortunately) larger than my office and I have enjoyed many chats/conservations/discussions with many people over the years. Thank you, dear colleagues, for your interest, for shedding light, for the distraction, for lifting me up, for your thoughts.

En dan nu natuurlijk mijn collega's bij Alterra. Op wat piekperiodes na was ik er eigenlijk zelden. Des te verrassender dat ik me bij jullie altijd thuis voel (misschien omdat ik alleen maar kom als er taart is...?). Na de afronding van mijn afstudeeronderzoek in 2000 ben ik de deur uitgelopen en toen ik in oktober 2006 weer binnenliep voelde het aan als een warm bad. En zo voelt het nog steeds. Dank voor jullie interesse en warmte.

For broadening and deepening my knowledge of many aspects involving biodiversity conservation, climate change and ecological modelling I owe many thanks to the opportunities granted by the ALTER-Net Network of Excellence and the PEER METIER Marie Curie Series of Events. In Palma de Mallorca, Leipzig, Bad Schandau, Peyresq and Brussels I have met many inspiring people, established scientists of great reputation as well as fellow young researchers, all radiant with energy and great ideas. Thank you all for embedding my research in the larger picture, for the discussions on science, society and politics. More importantly, thanks for inviting me back to a social and scientific life after the intense period following Jobbe's birth. I look forward to our next meeting.

De afleiding

Dit deel van mijn dankwoord wil ik graag beginnen met het noemen van Het Groene Wiel. Sinds najaar 2009 mag ik mij lid noemen van de vrijwillige productontwikkelingsgroep van deze Wageningse tak van Veldwerk Nederland. Op woensdagochtend, mooi halverwege de werkweek, werk ik (klets ik) met een (veel te) leuke groep mensen aan de ontwikkeling van lesproducten in het kader van de natuur- en milieueducatie op de Wageningse basisscholen. Heel mooi om samen een concrete, letterlijk tastbare bijdrage te leveren (tussen het praten door dus) aan dit onderwerp dat ik zo belangrijk vind: de kennis, opvoeding, ontwikkeling en het plezier van onze kinderen, over/voor/met en in de natuur. Fijn ook om een halve dag per week *niet* de verantwoordelijkheid te hebben voor het eindproduct en te zien dat dingen afkomen *zonder* dat ik er iets aan gedaan heb. Lieve Groenewielers, dankjewel voor de samenwerking, de gezelligheid en de mooie verhalen. Ik heb op veel fronten veel van jullie geleerd en ik verheug me op woensdag.

And now for many dear friends, most of them once nearby and now far off (and a single one nearby again - I hope many follow your good example Femke). With many lovely dinners and evenings filled with talk and laughter (and wine), with infrequent visits and infrequent phone calls, but lots of warmth, fun and silly stories, you have helped me take a step back, get my nose out of the everyday hassle and see and learn more of and in life than just work. Thank you all for your friendship.

En helemaal aan het eind van dit stuk komen we terecht bij de wortels. Pap en mam, Jan en Rita, jullie aandeel in dit stukje afleiding is tweeledig. Op de eerste plaats zorgen jullie, samen met Mieke en Thomas, Dionne en Jordi en mijn coole neefje en nichtje, voor vele mooie weekenden waarin we ongegeneerd onze voeten onder jullie goedgevulde dis steken en het kleine grut een moment aan jullie zorg over laten. Afleiding in optima forma: goede spijs, goede drank, goed gezelschap en een handvol koters. *Ik* ben klaar voor het barbecueseizoen. Daarnaast is er jullie aandeel in de facilitaire

dienstverlening: we kunnen altijd op jullie rekenen om een dag te komen helpen met een klusje of als oppas, waarmee jullie ons met grote regelmaat wat essentiële tijd voor elkaar gunnen. Dank jullie wel, voor de gastvrijheid, de onvoorwaardelijke hulp en de interesse.

De basis

Jobbe, je bent een bijzonder kind. Grappig, slim en overal voor in, uitzonderlijk sportief en behendig. Je bent een wonder, en belachelijk eigenwijs voor je leeftijd, altijd al geweest. Met jou werd ik moeder, met vallen en opstaan. De eerstgeborene. Wij maken er iets moois van samen.

Wesse, je bent een bijzonder kind. Rustig, schattig, maar overal voor in, uitzonderlijk geduldig en wat kun jij al goed blokken stapelen! Je bent een wonder, en belachelijk charmant voor je leeftijd, altijd al geweest. Met jou werd ik opnieuw moeder, nu gaat het vanzelf. De oogappel. Jij en ik, wij maken er iets moois van samen.

Samen zijn jullie onweerstaanbaar. Geen moeder, geen onderzoeker, geen mens kan zich betere afleiding wensen: luidruchtig, dwingend, onontkoombaar, totaal. Verliefd tot over mijn oren, op mijn eigen kinderen. Dank jullie wel.

Ingo. Dit is jouw plek, dat is duidelijk. Maar nu het zover is weet ik niet wat ik schrijven moet. Je bijdrage aan dit boek laat zich moeilijk kwantificeren. Dat het zonder jou minder goed en mooi zou zijn geweest is voor niemand een verrassing. Maar dat geldt voor mijzelf ook. Ik ben wie ik ben door mijn leven met jou. Waar ik ophoud en jij begint is allang niet meer duidelijk. Wie en waar ik zonder jou zou zijn geweest laat zich moeilijk raden. Gelukkig hoeft dat ook niet. Jij bent mijn man en misschien is daar wel alles mee gezegd. Nu ja, bijna alles. Dankjewel, voor jou, voor mij, voor de jongens. Ik zie een stralende toekomst. Al veertien jaar.

ABOUT THE AUTHOR

Marleen M.P. Cobben was born on 22 March 1979 in Geleen, The Netherlands. After her VWO-graduation at Stella Maris College in Meerssen, she studied Forest and Nature Management at Wageningen University from 1997 till 2002. She did her major in landscape ecology at Alterra, under the supervision of Jana Verboom. Marleen's minor was in GIS and remote sensing, and her internship at Oranjewoud in Oosterhout. In the last year of her studies, Marleen moved to Delft and worked there at several HRM departments of the Technical University of Delft. In the summer of 2004 she emigrated to Trondheim in Norway, where she worked as a freelance research assistant at the Norwegian Institute for Nature Research NINA for one and a half year. She started her PhD-study at Wageningen University in October 2006, initially stationed at the Norwegian University of Science and Technology NTNU. A year later she moved back to Wageningen, where in January 2008 her oldest son was born, and her second son in August 2010. During her PhD-study Marleen participated in the PEER METIER course Ecological Modelling and the ALTER-Net summer school. She co-organised an alumni meeting in 2009 for participants of the summer school. The results of her research are described in this PhD-thesis. Her paper in *Ecography* in 2011 has received the third prize in the Modelling Complex Ecological Dynamics Award in 2011 and the third prize in the NERN Best Paper Award in 2012. In April 2012 Marleen will start studying the effects of climate change on crop wild relatives as a postdoc at the Centre for Genetic Resources, The Netherlands. Marleen is a volunteer in the product development group of Het Groene Wiel in Wageningen, for the use of regional primary schools in their nature and environment education programmes.

PUBLICATIONS AND PRESENTATIONS

Scientific publications

Marleen MP Cobben, Jana Verboom, Paul FM Opdam, Rolf F Hoekstra, René Jochem, Marinus JM Smulders. 'Wrong place, wrong time: climate change-induced range shift across fragmented habitat causes maladaptation and declined population size in a modelled bird species', accepted by *Global Change Biology*.

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M.M.P. Cobben, J. Verboom, P.F.M. Opdam, R.F. Hoekstra, R. Jochem, P. Arens, M.J.M. Smulders (2011) 'Projected climate change causes loss and redistribution of neutral genetic diversity in a model metapopulation model of a medium-good disperser', *Ecography* 34: 920-932.

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Alterra report

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Specialist publication

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Oral presentations

M.M.P. Cobben, J. Verboom, P.F.M. Opdam, R.F. Hoekstra, R. Jochem, P. Arens, M.J.M. Smulders. 'Evolution and distribution of dispersal probabilities in metapopulations under climate change'. European Ecological Federation Congress, 25-29 September 2011, Ávila, Spain

M.M.P. Cobben, M.J.M. Smulders, J. Verboom, P. Opdam, R. Hoekstra. 'Genetic processes in fragmented landscapes under climate change'. Final stakeholder meeting A2 project Klimaat voor Ruimte, 14 October 2010, Woerden, The Netherlands

M.M.P. Cobben, J. Verboom, P. Opdam, R. Hoekstra, M.J.M. Smulders. 'Modelling climate impacts on genetic diversity in metapopulations'. Netherlands Annual Ecology Meeting, 9-10 February 2010, Lunteren, The Netherlands

M.M.P. Cobben, M.J.M. Smulders, J. Verboom, P. Opdam, R. Hoekstra. 'Modelling climate impacts on genetic diversity in metapopulations'. METIER Final Conference 'Climate-Water-Biodiversity-Land Use: Young Scientists Tackling Complex Environmental Challenges', 4-6 November 2009, Brussels, Belgium



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C E R T I F I C A T E

The Netherlands Research School for the
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born on 22 March 1979 in Geleen, The Netherlands

has successfully fulfilled all requirements of the
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Wageningen, 17 April 2012

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- o Environmental Research in Context
- o Research Context Activity: Volunteer at Het Groene Wiel (Wageningen), specifically co-developing the biodiversity game and a publication in *Natuur aan de Basis* (2009 – 2012).
- o Alternet Summer School on Biodiversity and Ecosystem Services

Other PhD courses

- o Scientific Writing
- o Information Literacy
- o Effective Behaviour in your Professional Surroundings
- o Alternet Science Communication course
- o NWO Talent Class Kernachtig Formulieren
- o PEER: METIER Training Course Ecological Modelling
- o Mobilising your Scientific Network
- o Career Assessment

Oral Presentations

- o The Netherlands Annual Ecology Meeting (NAEM), 8 February 2010, Lunteren, The Netherlands
- o PEER: METIER Final Conference "Climate - Water - Biodiversity - Land Use: Young Scientists Tackling Complex Environmental Challenges", 4 – 6 November 2009, Brussels, Belgium
- o 12th Congress of The European Ecological Federation (EEF), 25 – 29 September 2011, Ávila, Spain

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Mr. Johan Feenstra

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